THE SYSTEMATICS AND EVOLUTION OF *LUDWIGIA* SECT. *MICROCARPIUM* (ONAGRACEAE)[1]

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ABSTRACT

Ludwigia sect. *Microcarpium*, which consists of 14 species distributed mainly in the southeastern United States, is the second-largest section in the genus, the largest being the phylogenetically central sect. *Myrtocarpus* of South America.

Plants of *Ludwigia* sect. *Microcarpium* are morphologically diverse; they form a polyploid complex of four diploids, eight tetraploids, two hexaploids, and one octoploid. They are facultatively autogamous herbaceous plants capable of reproducing both sexually and asexually (forming stolons late in the flowering season). Based on extensive crossing experiments as well as field and herbarium studies, the relationships among species of this section have been clarified. Internal genetic barriers between species are nonexistent, and natural hybridization is fairly common.

Among the diploid species, *L. linifolia* and *L. linearis* have very narrow leaves, petaliferous flowers, and elongate capsules. The two species, however, differ chromosomally by one reciprocal translocation. F_1 hybrids between them are vigorous, have ca. 50% stainable pollen, and produce moderate quantities of viable seeds. *Ludwigia stricta*, the Cuban endemic, is apparently most closely allied to *L. linifolia*, based on morphological evidence, but has not yet been studied biosystematically. *Ludwigia microcarpa*, in contrast, has spatulate-obovate leaves, small, apetalous flowers, and minute obconical capsules. Artificial hybrids between *L. microcarpa* and either *L. linearis* or *L. linifolia* form neither stainable pollen nor seeds; for the most part, the chromosomes of these hybrids do not pair in meiosis. *Ludwigia microcarpa* probably evolved relatively early from outcrossing ancestors.

Although the nine tetraploid members in sect. *Microcarpium* are sharply distinct morphologically, they can be crossed in any direction in the experimental greenhouse and form fertile F_1 offspring. Natural hybrids in plants of this group are also fairly common and in some cases blur the boundaries of the species. Somewhat surprisingly, none of the extant diploid species are considered to be direct ancestors of the tetraploids, based on cytogenetic studies.

The two hexaploid species, *L. alata* and *L. simpsonii*, are not closely related to each other. The affinity of *L. alata* is definitely with the tetraploid species group. Hybrids between *L. alata* and any other tetraploid species consistently exhibit a modal configuration of 16 II and 8 I in meiosis. Based on its morphology and the cytology of hybrids involving it, *L. alata* may have originated through hybridization between a tetraploid species, possibly *L. lanceolata*, and the diploid *L. microcarpa*, or populations ancestral to each of these species.

Ludwigia simpsonii, on the other hand, is closely related to *L. curtissii*, which is the only octoploid in sect. *Microcarpium*. The two species are unique in sect. *Microcarpium* in having loculicidal capsules and, together with the diploid *L. microcarpa*, in having spatulate-obovate cauline leaves. Cytogenetic and morphological studies suggest that the octoploid *L. curtissii* may have resulted from hybridization of *L. simpsonii* and a petaliferous diploid species, possibly *L. linifolia*, *L. linearis*, or populations like them. *Ludwigia microcarpa* is involved in the formation of the hexaploid *L. simpsonii* and therefore that of the octoploid *L. curtissii*. The other progenitors of *L. simpsonii* are not clear, but some species in sect. *Dantia* or populations ancestral to them with apetalous flowers, opposite leaves, and a prostrate habit are likely candidates.

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To summarize, recombination from somewhat differentiated populations, followed by polyploidization and the maintenance of well-adapted genetic strains by a combination of autogamy and vegetative reproduction, appears to have played a central role in the evolution of the species of *Ludwigia* sect. *Microcarpium*.

Ludwigia is a distinct genus of Onagraceae and is the only member of Jussiaeeae. Fossil records of pollen suggest that it is archaic and has existed at least 50 million years since the middle Eocene in both the Northern and Southern hemispheres (Gonzales Guzmán, 1967; Rouse, 1962; Bratseva, 1969). Except for its chromosome structure and number, which appear to be relatively specialized (Kurabayashi et al., 1962), *Ludwigia* is one of the least specialized genera as to wood anatomy (Carlquist, 1975, 1982), floral anatomy (Eyde, 1977, 1978, 1981), and leaf anatomy (Keating, 1982). Based primarily on its unusual nectary position, ovular vasculature, and independently derived epigyny, Eyde (1977, 1978, 1981) demonstrated that *Ludwigia* represents a distinct branch from the common ancestor of the family, with all other living genera on the other branch; in Hennigian terms, it is the sister group of the remainder of the family.

The genus *Ludwigia* comprises 82 species that are diverse enough, especially in fruit, seed, and flower characters, to be classified in 23 sections, 14 of which are monotypic (Raven, 1963; Ramamoorthy & Zardini, 1987). Plants of *Ludwigia* are adapted to wet habitats in the tropics and subtropics. They probably originated in South America, the most important center of diversity for *Ludwigia*, and the area where the most primitive species are found (Ramamoorthy & Zardini, 1987). The genus, however, is also well represented in temperate North America and has three endemic species in temperate Asia.

In North America, there are 23 native *Ludwigia* species, characterized by having convex or elevated nectaries, tetramerous, haplostemonous flowers, pluriseriate ovaries, free seeds with narrow raphes, and herbaceous habits. Most of these plants are confined to the Atlantic and Gulf coastal plains of the United States, although some species are more widespread, and some extend into the islands of the Caribbean; one is endemic in Cuba. Based primarily on characters of capsules, mode of perennation, and phyllotaxy, the North American plants are classified into sect. *Ludwigia* (4 species), sect. *Dantia* (DC.) Munz (5 species), and sect. *Microcarpium* Munz (14 species). Table 1 summarizes the diagnostic characters of these three sections.

Based on his study of the structure and morphology of the capsules and nectaries of *Ludwigia*, Eyde (1981) considered sections *Dantia* and *Microcarpium* to comprise a closely knit group derived from the phylogenetically central, diplostemonous *Myrtocarpus* complex, whereas sect. *Ludwigia* is different enough to have arisen independently from the *Myrtocarpus* complex.

Section *Microcarpium* was selected for the present revision because it is the second-largest section of *Ludwigia* and is very diverse, because it has not been revised in light of recent new data and evolutionary concepts, and because several species of this section are variable and taxonomically difficult, with boundaries between species often blurred by intermediates.

The purposes of this revision are to clarify species limits, to determine the degree and significance of natural hybridization, and to analyze natural affinities among species of sect. *Microcarpium*. Toward this end, more than 7,000 specimens from 44 herbaria have been consulted for morphological studies and for mapping. Furthermore, I have made three extensive field studies in the coastal plains of the southeastern United States. Searches for possible natural hybrids were made in the field whenever taxa occurred sympatrically. Seeds and/or clonal transplants of all species were propagated at the Missouri Botanical Garden for chromosome determination and morphological study.

Taxonomic History

After the establishment of the genus *Ludwigia* in 1753 by Carl Linnaeus, the first group of North American species of sect. *Microcarpium* was discovered by the British botanist Thomas Walter (1788). Four of his species are currently recognized: *L. glandulosa*, *L. linearis*, *L. pilosa* (including *L. rudis*), and *L. suffruticosa*.

Jean Baptiste A. P. M. de Lamarck (1789, 1792) published "*Jussiaea brachycarpa*" and "*Ludwigia hirsuta*," based on materials collected from South Carolina. These names are synonyms of *L. glandulosa* and *L. pilosa* respectively, as Lamarck himself suspected.

The next botanist to study North American *Ludwigia* was Andre Michaux (1803), who described nine species of *Ludwigia* in his *Flora Boreali-Americana*. Of these, *L. microcarpa* is a member of sect. *Microcarpium*.

In 1814, Jean L. M. Poiret correctly added the

TABLE 1. Comparison of the native North American sections of *Ludwigia*.

Character	Sect. *Ludwigia* (4 species)	Sect. *Dantia* (5 species)	Sect. *Microcarpium* (14 species & 1 subspecies)
Habit	Perennial. Plants erect, lacking stolons; roots tuberous	Perennial. Plants creeping, rooting at nodes; roots fibrous	Perennial. Plants erect, usually stoloniferous (rhizomatous in one species); roots fibrous
Phyllotaxy	Leaves alternate	Leaves opposite	Leaves alternate
Capsules	Capsules pedicellate, opening by a terminal pore formed after abscission of the style base	Capsules sessile or pedicellate, irregularly dehiscent	Capsules sessile or short-pedicellate, ring-, loculicidal-, or peeled-dehiscent (see text)
Seed surface	Cells in parallel columns, transversely elongate to the seed length	Cells in parallel columns, transversely elongate to the seed length	Cells ± isodiametric or in parallel columns and either longitudinally or tranversely elongate to the seed length
Petals	Petals 8–15 mm long	Petals lacking or 2–10 mm long	Petals lacking (in 3 species 3–6 mm long); vestigial petals occasionally present in some primarily apetalous species
Nectaries	4 shallow ciliate depressions on the raised summit of the ovary, alternating with the sepals and stamens	4 raised and rounded lobes, surrounding the style base and alternating with the sepals and stamens	4 raised and rounded lobes, surrounding the style base and alternating with the sepals and stamens
Chromosome numbers	$n = 8$ (4 species)	$n = 8$ (1 species) $n = 16$ (2 species) $n = 24$ (2 species)	$n = 8$ (4 species) $n = 16$ (7 species & 1 subspecies) $n = 24$ (2 species) $n = 32$ (1 species)
Pollen grains	Shed as tetrads	Shed singly or as tetrads	Shed singly or as tetrads
Genetic compatibility	Self-compatible	Self-compatible	Self-compatible

new species *L. linifolia*, collected in the southern United States; it resembles but is quite distinct from *L. linearis*.

It was not until 1821 that the species of sect. *Microcarpium* were described by American botanists. Of the four species in sect. *Microcarpium* that Steven Elliott (1816–1821) described, *Ludwigia alata*, *L. sphaerocarpa*, and *L. lanceolata* are currently recognized, whereas *L. cylindrica* represents a synonym of *L. glandulosa* Walter. Although Elliott correctly differentiated *L. alata* from *L. lanceolata*, the striking superficial resemblance of the two species, especially in dried herbarium specimens, has constantly been a source of confusion among botanists (Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982; Clewell, 1985). The great distinctiveness of these two species in such characters as floral morphology, pollen and seed surface features, and chromosome numbers were only appreciated recently (Peng, 1988, and this study).

In 1836, *Ludwigia polycarpa*, a distinctive member of sect. *Microcarpium* distributed mainly in the northcentral United States, was discovered in Kentucky by Charles Wilkins Short and Robert Peter.

Shortly thereafter, John Torrey and Asa Gray (1838–1840), in *A Flora of North America*, proposed two varieties in sect. *Microcarpium*, i.e., *Ludwigia cylindrica β brachycarpa* and *L. capitata β pubens*. The former is currently recognized as the small-fruited, western subspecies of *L. glandulosa* (Peng, 1986), whereas the latter represents a natural hybrid between *L. suffruticosa* and *L. pilosa* (Peng, 1988).

In 1845, George Engelmann and Asa Gray described a densely pubescent variety of *Ludwigia linearis* from Texas. Owing to the complex variation pattern and the many intermediate populations found in the range of this species, however, the variety is not recognized in the present study.

Ludwigia stricta, the only Cuban endemic in

sect. *Microcarpium*, became known when August Grisebach (1866) described *Isnardia stricta* in *Catalogus Plantarum Cubensium*. The correct combination in *Ludwigia* was made by Francisco Adolfo Sauvalle (1873) in the *Flora Cubana*.

Alvin Wentworth Chapman added *Ludwigia curtissii* (1883) and *L. simpsonii* (1892) to the genus in his study of the flora of the southern United States.

John Kunkel Small named *Ludwigia simulata* in 1903, not knowing that it represented the hybrid *L. pilosa* × *L. lanceolata*. In 1933, he grouped, for the first time, plants of *Ludwigia* sect. *Microcarpium* under "Microcarpeae," and described from the Everglades of Florida *L. spathulifolia*, which has now been merged with *L. curtissii*.

Burghard Helwig in 1928 published *Ludwigia cubensis* from Cuba, which, however, is now considered as conspecific with *L. simpsonii* from Florida.

Merritt Lyndon Fernald and Ludlow Griscom (1935) described three additional varieties for the highly polymorphic *Ludwigia sphaerocarpa*, which itself may have originated as a result of hybridization and which now intergrades with *L. pilosa* freely (Peng, 1988). These hybrids are not recognized in this paper for reasons discussed elsewhere.

Paul Munz's monograph (1944, 1965) contained the most comprehensive treatment of North American *Ludwigia* in his time. In the 1944 paper, he formally delimited sect. *Microcarpium*. His concept has since been widely accepted. James Allan Duke (1955) was the first author to indicate and to provide examples of natural hybridization among North American species of *Ludwigia*.

In the course of my biosystematic study of *Ludwigia* sect. *Microcarpium*, a number of atypical specimens initially identified as *L. pilosa* Walter were shown to be a new species, which I subsequently named *L. ravenii* (Peng, 1984). This represents the last named species of sect. *Microcarpium*, and makes the total number of species of this section 14.

Morphology

Habit

All species in *Ludwigia* sect. *Microcarpium* are erect perennial herbs ranging from about 15 to 100 cm tall. Leafy, usually unbranched stolons are produced from the base of erect stems. The stolons creep along the surface of moist ground or float on water late in the flowering/fruiting season. Some species, however, may also send out stolons in the summer while they are actively flowering or even throughout their growing season. The stolons can be long (up to 2.5 m) and stout as in *L. pilosa* or short (5–15[–20] cm) and slender as in *L. microcarpa* and *L. ravenii*. The stolons give rise to erect shoots from their tips when the growing season resumes. In *L. polycarpa* the stolons are normally up to 15 cm long, and with leaves densely congested at the apex of stolons, overlapping one another and thereby protecting the apical meristem. This is apparently an adaptation to the severe winter that plants of *L. polycarpa* have to endure in the northern States. In *L. suffruticosa* stolons are uncommon. Instead, perennation is mainly by thick, somewhat woody, branched rhizomes. New shoots arise from the nodes of the rhizomes in growing season. It may be that in drier sandy situations, the plants persist by rhizomes, whereas in wet situations, the plants send out stolons.

In *Ludwigia curtissii* and *L. simpsonii*, stolons are rarely formed; the plants simply produce new shoots, which are ascending or decumbent at first and soon become erect from the base of the previous year's stem. They may not need to overwinter with low-profile stolons, as they are distributed mainly in Florida and the Caribbean Islands where the growing season is long and the winter is not severe.

Stems

Stems are usually well branched in most species of *Ludwigia* sect. *Microcarpium*. Plants of *L. suffruticosa* are, however, often simple. When they branch, the branches are few and usually arise from upper leaf axils beneath the compact inflorescences and characteristically overtop the main flowering/fruiting stems. Unbranched flowering stems are seen also in some populations of *L. curtissii*, *L. linifolia*, *L. microcarpa*, *L. simpsonii*, and *L. stricta*. The stems of some plants of *L. microcarpa* are distinctly zigzag. The stems of most species are slightly ridged; those of *L. alata* and *L. microcarpa* are often conspicuously ridged or winged. *Ludwigia pilosa* is the only species with nearly terete stems. The lower part of the stems of all species, when entirely submerged, is swollen and spongy.

Pubescence

Many species in *Ludwigia* sect. *Microcarpium* are glabrous to subglabrous; the margins of leaf, sepal, or bracteoles, and surfaces of fruit may sometimes be minutely strigillose or minutely papillose. Only *L. ravenii* and *L. pilosa* are consis-

tently hirtellous throughout. *Ludwigia sphaerocarpa*, a species that intergrades substantially with *L. pilosa*, is variable in many aspects, especially pubescence. Populations of *L. sphaerocarpa* range from being completely glabrous to densely strigillose throughout. Similarly variable is *L. linearis*, but no interspecific hybridization has apparently played a role here. The pattern of the distribution of hairs in *L. suffruticosa* is especially interesting: some plants are completely glabrous; some plants are hirtellous either on the terminal inflorescence or on the basal stems (including stolons/rhizomes), or both, but are otherwise glabrous.

The following are the main types of pubescence:

1. *Minutely puberulent.* Hairs exceedingly short, fine, straight, erect to ascending, sparse or dense, 0.02–0.1 mm long, found occasionally in plants of *Ludwigia linearis*, *L. sphaerocarpa*, on fruits of *L. microcarpa*, and less commonly on fruits of *L. simpsonii*, *L. curtissii*, and *L. suffruticosa*.

2. *Strigillose.* Hairs coarse, translucent, unicellular, 0.1–0.6 mm long, appressed to ascending; found in some populations of *Ludwigia sphaerocarpa* and *L. linearis*.

3. *Minutely strigillose.* Similar to strigillose pubescence, but the hairs more slender and shorter, ranging from 0.02 to 0.1 mm long. Frequently seen on sepals, bracteoles, and leaves of various species; also on the wings of capsules in *Ludwigia lanceolata* and capsules of both subspecies of *L. glandulosa*, and occasionally of *L. polycarpa*.

4. *Minutely papillose.* Blunt-tipped, minute projections from the surface, ca. 0.02–0.03 mm in length. This hair type is found occasionally on the margins of leaves and sepals, on fruit walls, and on nectary discs. It may be difficult to distinguish from minutely strigillose hair when the latter is exceedingly short.

5. *Hirtellous.* Hairs coarse, stiff, straight, erect to spreading, with an attenuate apex and a slightly broadened base, 0.25–0.95 mm long, translucent or spotted with light brown pigments. Hairs of this type are typical of *Ludwigia pilosa*, *L. ravenii*, and occasionally of *L. sphaerocarpa*, as well as part of the plant body of *L. suffruticosa*.

LEAVES

The leaves are simple and alternate. *Ludwigia simpsonii* is exceptional in frequently having some opposite or subopposite leaves at the lower nodes or in the seedling stage, a feature that might be related to the derivation of one or more of its genomes from plants of the opposite-leaved sect. *Dantia* (see below). The leaves on the rhizomes of *L. suffruticosa* are small and scalelike. Those on stolons are mostly elliptic- to rhombic-obovate or suborbicular (narrowly elliptic to narrowly oblanceolate in *L. linearis* and *L. linifolia*). These are usually broader and shorter than the cauline leaves, which are usually narrowly lanceolate to lanceolate, occasionally elliptic or oblanceolate, and often gradually reduced and narrower up the stem. *Ludwigia linearis* and *L. linifolia* have sublinear leaves. In *L. curtissii*, *L. microcarpa*, and *L. simpsonii*, the leaves range from (narrowly) spatulate-oblanceolate to spatulate-obovate or spatulate.

The leaves of all species of sect. *Microcarpium* are sessile or nearly so and either narrowly cuneate or attenuate basally. *Ludwigia suffruticosa* is exceptional in having a rounded to obtuse leaf base.

As in *Ludwigia* sect. *Myrtocarpus* sensu lato (Ramamoorthy & Zardini, 1987), the leaf margin is usually subentire, with a few glandular reddish or pink teeth that have an unusual hydathodal structure (Castells et al., 1979; Keating, 1982); such teeth are especially evident in *L. microcarpa*.

The secondary veins of leaves are usually obscure adaxially and distinct abaxially in sect. *Microcarpium*. In the closely allied *Ludwigia linifolia* and *L. stricta* and in *L. simpsonii* and *L. curtissii*, the secondary veins are, however, faint on both sides of the leaves. *Ludwigia linearis*, having narrow leaves like the related *L. linifolia*, has, by contrast, on its abaxial leaf surface very evident secondary veins, which anastomose and form a pair of marginal veins along the margins.

INFLORESCENCE

The flowers are sessile or shortly pedicellate and borne singly in the (usually upper) leaf axils of the main stem and the branches. In *Ludwigia suffruticosa*, the flowers are congested in very compact terminal spikes or racemes. The leaves subtending the flowers are much reduced and bractlike. As stems of this species remain single or have only a few branches, there are only one to several such inflorescences per plant. In most other species, the stems are well branched, and the flowers are axillary and usually very abundant. In *L. alata* and *L. pilosa*, the flowers are sometimes quite congested on the upper parts of branches. In *L. polycarpa* and *L. glandulosa*, one to a few very short branches heavily laden with flowers/fruits are often seen from the very base of primary branches. This frequently gives an appearance of several flowering branches arising simultaneously from the nodes of the main stem.

PEDICELS

The flowers and fruits are nearly sessile in most species. Pedicels (measured from the base of mature fruits), when present, are usually up to 0.5 (–1) mm long. Pedicels of *Ludwigia suffruticosa* and *L. sphaerocarpa* range 0.5–1.5(–2.3) mm long. Populations of *L. linearis* from west of the Mississippi River often have distinct pedicels up to 3.5(–5) mm long.

BRACTEOLES

Bracteoles are present in pairs near the base of the ovary in all species. They are succulent and are flanked by a pair of reddish or dark purplish, glandlike stipels on their base. A small swollen emergence located immediately below the bracteole is apparently an extension of the bracteole base and is prominent in some species, especially *Ludwigia curtissii*, *L. lanceolata*, *L. microcarpa*, and *L. simpsonii*. This character is more evident in live plants than in herbarium specimens.

Despite often being variable in length, even within the same plant (in *Ludwigia linifolia*, the bracteoles range (1.5–)2.5–9(–13) mm long), a few species, including *L. glandulosa*, *L. microcarpa*, and *L. sphaerocarpa*, consistently have shorter bracteoles (less than 1.5 mm long) than those of the other species (Table 2). The bracteoles are located either at the base or higher up on the sides of the capsules. In *L. sphaerocarpa* and occasionally in *L. glandulosa*, *L. linearis*, and *L. suffruticosa*, however, the bracteoles are found on the short pedicels.

FLOWERS

Of the 15 taxa of sect. *Microcarpium*, only three diploid species are petaliferous, although vestigial petals may occasionally appear in a few flowers of polyploid species (Table 2). Flowers are consistently tetramerous, pentamerous flowers being exceptional.

SEPALS

Sepals are entire, but may be minutely strigillose along the margins in some species. Unlike plants of sect. *Myrtocarpus* sensu lato (Ramamoorthy & Zardini, 1987), the sepals persist even after the capsules mature and dehisce. Sepals are greenish in most species, but they are creamy white on the adaxial surface in *L. alata*, *L. pilosa*, and *L. suffruticosa* and are yellowish on the adaxial surface in *L. sphaerocarpa*.

PETALS

Petals are yellow, small, narrowly obovate to subrotund, and range from 2.5 to 6 mm long and from 1.2 to 5 mm wide. They fall off a few hours after anthesis, which occurs early in the morning, and are usually gone by noon. All petaliferous species are able to effect mechanical self-pollination. My field experience, however, did not allow me to judge whether these plants attract significantly more insect pollinators than other apetalous species with showy sepals.

STAMENS

Most species of *Ludwigia* are consistently either haplostemonous (stamens in one whorl) or diplostemonous (stamens in two whorls) (Ramamoorthy & Zardini, 1987). All species of sect. *Microcarpium* are haplostemonous, which is a derived condition. The stamens are antesepalous, situated between the sepal base and the nectary discs.

ANTHERS

The anthers vary from 0.1 mm long in *Ludwigia microcarpa* to 2 mm long in *L. linearis*. *Ludwigia linearis* is unique in sect. *Microcarpium* in having polysporangiate anthers partitioned horizontally by septa that include both tapetum and parenchyma (Tobe & Raven, 1986). Such specialization is shared only by *L. latifolia*, an unrelated South American species of sect. *Tectiflora*, and five other genera of Onagreae. It is worth noting, however, that these septa in the anthers disintegrate and result in a continuous sporogenous tissue before the anthers dehisce. Many conspicuous vestiges of the disintegrated septa are visible on the inner surface of the anther wall at this stage.

POLLEN

The pollen of *Ludwigia* sect. *Microcarpium* is quite uniform, being characterized by isopolar grains frequently with prominent colpal extensions and with a psilate exine (Praglowski et al., 1983). Five species of sect. *Microcarpium*—*L. alata*, *L. curtissii*, *L. microcarpa*, *L. simpsonii*, and *L. suffruticosa*—shed their pollen singly, whereas the other nine species shed their pollen in tetrads (Table 2). This character is of some taxonomic value. For example, it can be used along with seed-surface pattern to distinguish *L. alata*, which sheds its pollen singly, from *L. lanceolata*, which sheds its pollen as tetrads. These two species are similar in general aspect and in their obpyramidal, winged

TABLE 2. Diagnostic characters of species and subspecies of *Ludwigia* sect. *Microcarpium*.

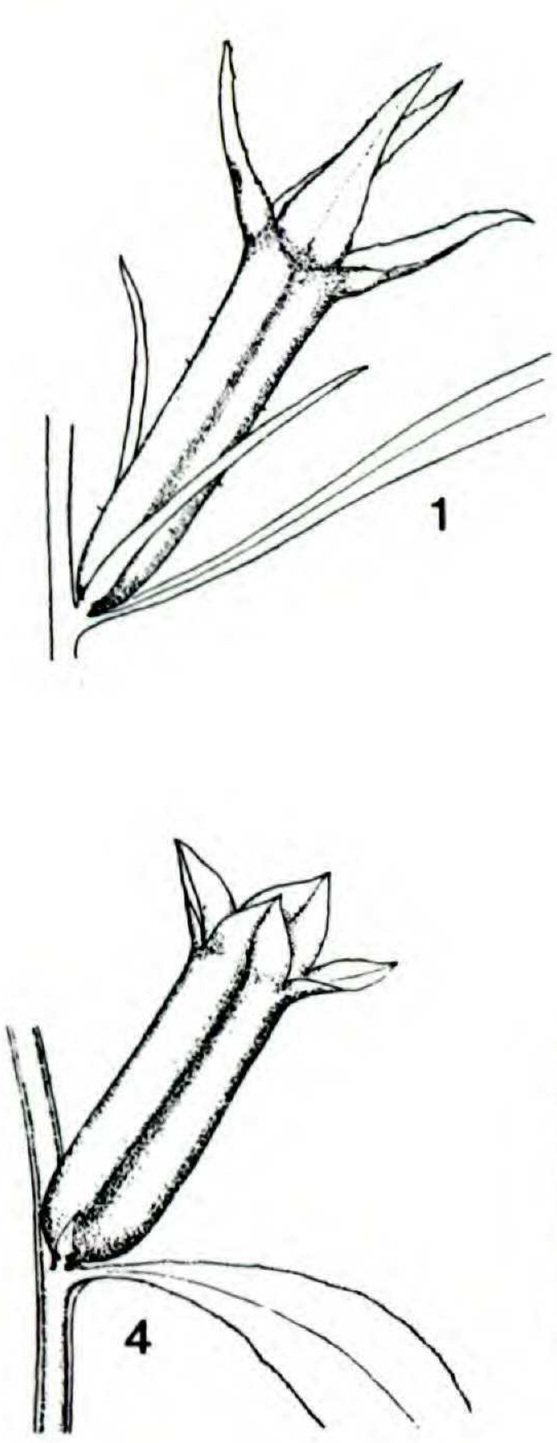
Taxon with Chromosome Number	Petals Present (+) or Absent (−)	Pollen Grains Shed Singly (S) or as Tetrads (T)	Overall Pubescence	Capsule Length (mm)	Capsule Shape	Bracteole Length (mm)	Seed Surface Cell Shape and Orientation[1]
L. linifolia, $n = 8$	+	T	Glabrous	6–12	Subcylindric	(1.5)3–10(–13)	I
L. sticta, $n = 8$	+	T	Glabrous	5–6.5	Subcylindric	1–2.5	I
L. linearis, $n = 8$	+	T	Glabrous to densely strigillose	6–10	Elongate-obpyramidal	0.5–2.5	P or T[4]
L. glandulosa subsp. *glandulosa*, $n = 16$	−	T	Glabrous but sparsely strigillose on stem and fruit	(4–)5–8	Subcylindric	0.5–1.2	P
subsp. *brachycarpa*, $n = 16$	−	T	Glabrous, but strigillose on stem and fruit	2–4	Subcylindric	0.4–0.8	T
L. polycarpa, $n = 16$	−	T	Glabrous	(4–)4.5–7	Oblong-obovoid	3.5–7.5	P
L. suffruticosa, $n = 16$	−	S	Glabrous except the inflorescence and stem base, which are sparsely hirtellous	3.5–4	Obpyramidal with rounded corners	(3–)4–5.5(–6.5)	I
L. lanceolata, $n = 16$	−	T	Glabrous	(3.5–)4–5	Obpyramidal, 4-winged	1.5–4.3	I
L. alata, $n = 24$	−	S	Glabrous	3–4	Obpyramidal, 4-winged	2.5–4.5	T
L. sphaerocarpa, $n = 16$	−	T	Glabrous to densely strigillose	2–4.5	Subglobose	0.5–1.5(–2.5)	P and T[4]
L. pilosa, $n = 16$	−	T	Hirtellous	(3–)3.5–5	Subglobose to oblong-obovoid	2.5–7.2	I
L. ravenii, $n = 16$	−	T	Hirtellous	(3–)4–5.3	Oblong-obovoid	(1.5–)2–4.3	T
L. microcarpa, $n = 8$	−	S	Glabrous	1–1.5	Obpyramidal with rounded corners	0.3–1(–1.5)	T
L. simpsonii, $n = 24$	−	S	Glabrous	1.5–2(–2.5)	Broadly turbinate	1–2.5	T
L. curtisii, $n = 32$	−[2]	S	Glabrous	(2–)2.5–4.5	Turbinate	1.5–4.5	T

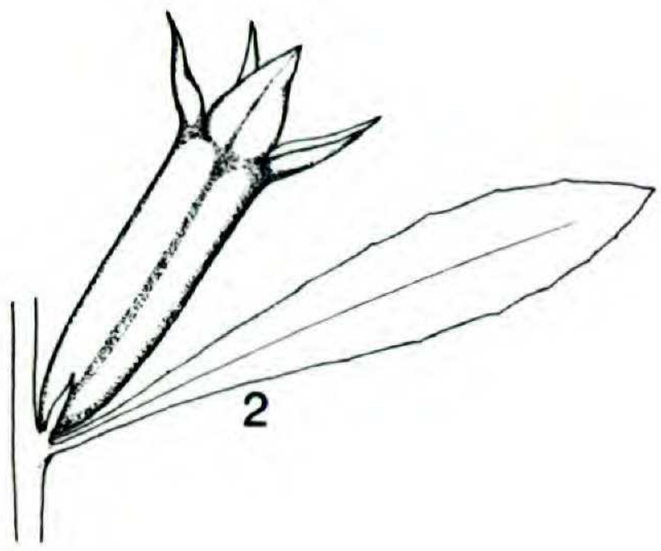
[1] Letter codes I, P, and T indicate seeds with surface cells more or less isodiametric (I), in columns elongate parallel to the seed length (P), and elongate transversely to the seed length (T).

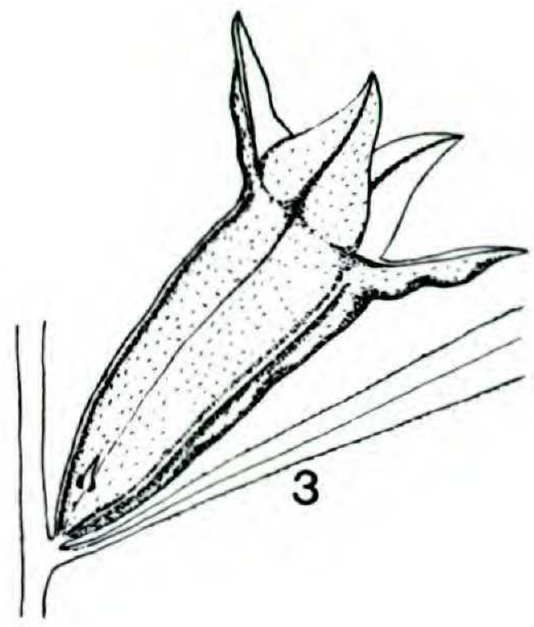
[2] Flowers with 1–3(–4) vestigial petals sometimes observed.

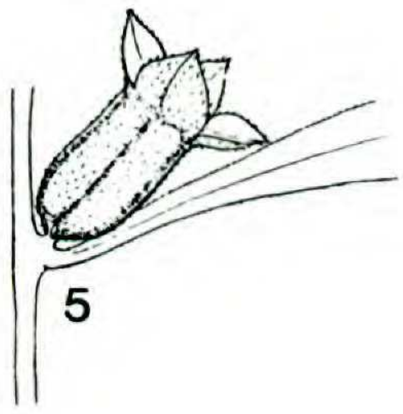
[3] Seed surface cells elongate parallel to the seed length are predominantly exhibited by more glabrous populations, whereas cells elongate transversely to the seed length are prevalent in more strigillose populations.

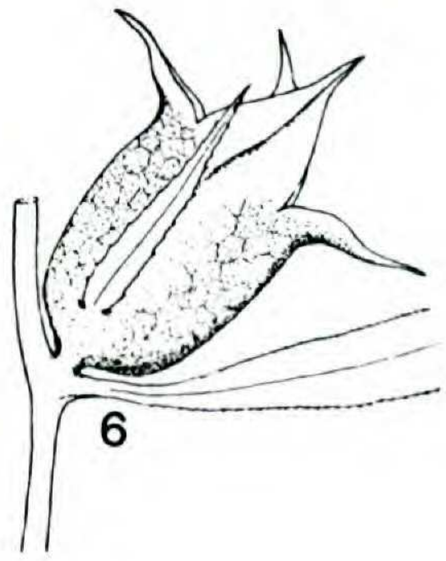
[4] Seed surface shows a mixture of cells elongate parallel or transversely to the seed length. Sometimes the orientation of these columnar cells is irregular.

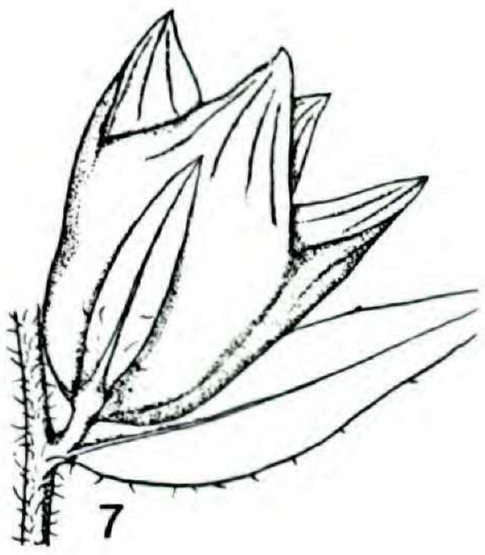


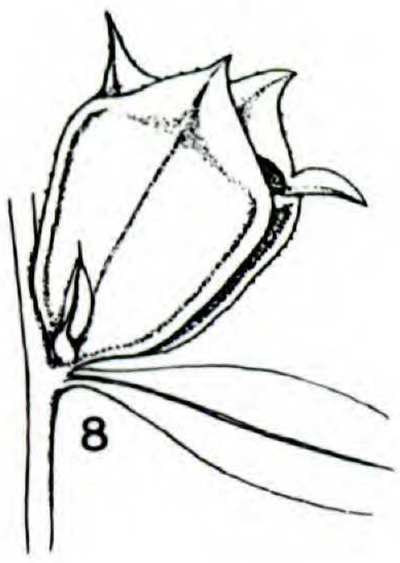


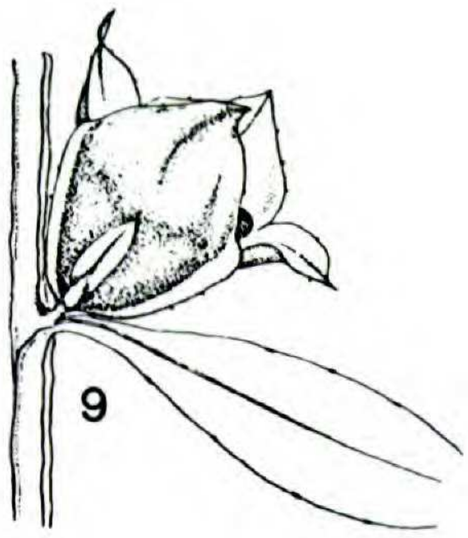


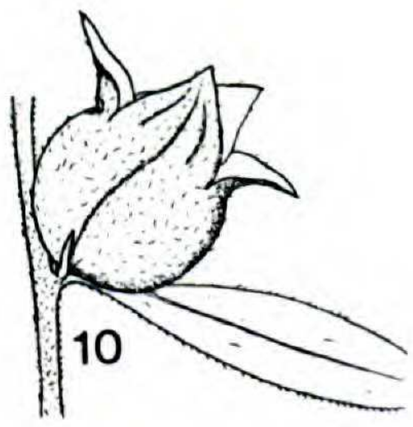


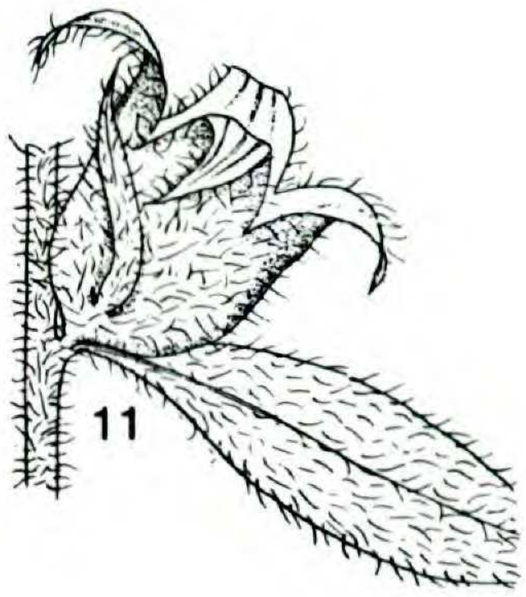


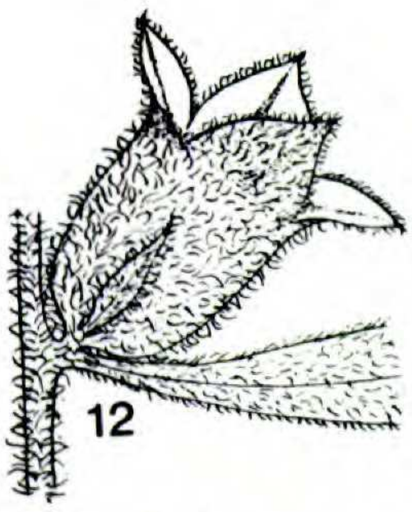


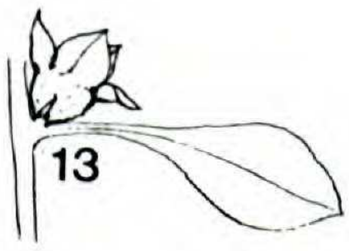


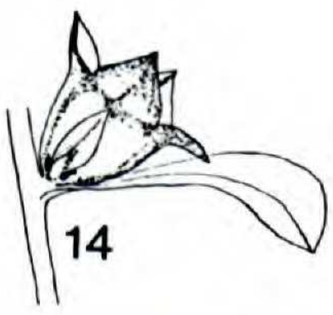


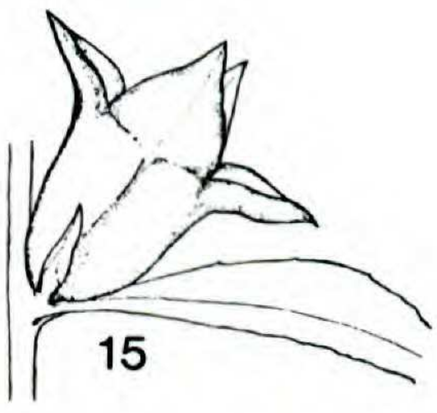






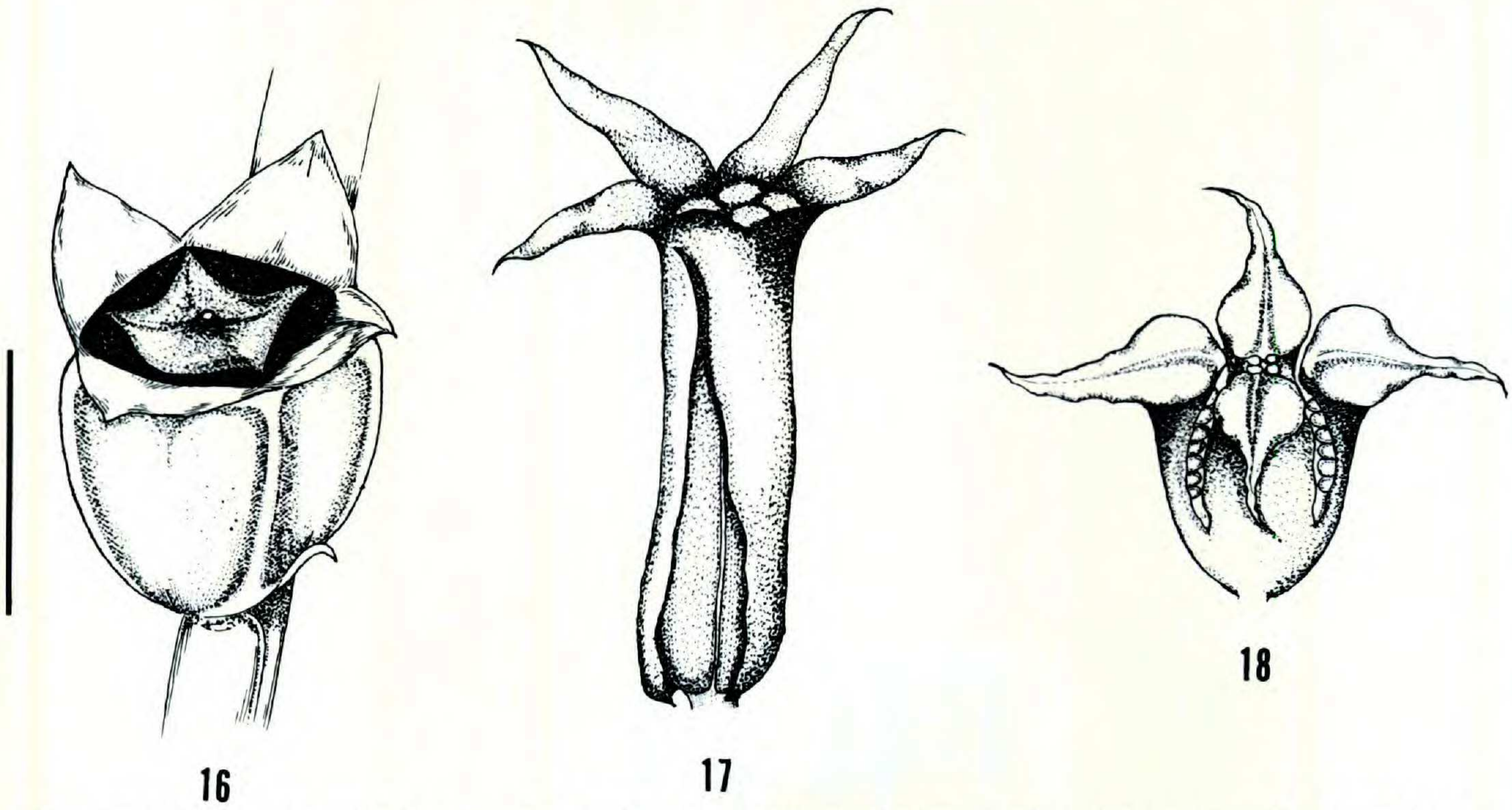






FIGURES 1–15. Mature fruits of *Ludwigia* sect. *Microcarpium*.—1. *L. linifolia*.—2. *L. stricta*.—3. *L. linearis*.—4. *L. glandulosa* subsp. *glandulosa*.—5. *L. glandulosa* subsp. *brachycarpa*.—6. *L. polycarpa*.—7. *L. suffruticosa*.—8. *L. lanceolata*.—9. *L. alata*.—10. *L. sphaerocarpa*.—11. *L. pilosa*.—12. *L. ravenii*.—13. *L. microcarpa*.—14. *L. simpsonii*.—15. *L. curtissii*. Drawn from living plants cultivated at the Missouri Botanical Garden.

fruits, and are superficially difficult to separate. The mode in which pollen is shed is useful to detect natural hybrids when their putative parents differ in this respect. Such hybrids generally exhibit both modes of pollen dispersal or pollen in very loose tetrads. Finally, the percentage of stainable pollen is useful to detect sterile hybrids or hybrids with reduced fecundity.



FIGURES 16–18. Capsular dehiscence in *Ludwigia* sect. *Microcarpium*. —16. *L. lanceolata*. —17. *L. linifolia*. —18. *L. curtissii*. Scale line equals 4 mm. Drawn from living plants cultivated at the Missouri Botanical Garden.

DISCS

One of the important characters that allows *Ludwigia* to be recognized as the sister group to all other genera of Onagraceae is that its nectary disc is situated on the summit of the ovary. By contrast, all other onagraceous plants have nectaries at the base of the floral tube; the nectaries, therefore, are androecial (Eyde, 1981).

The discs of *Ludwigia* sect. *Microcarpium* are shallowly dome-shaped, and they occur on the apex of the ovary. They are more or less distinctly four-lobed, the lobes alternating with the stamens, and are antepetalous (in petalous species). They are usually yellow or greenish at anthesis and turn dark reddish purple in fruit. In most species the discs are glabrous. *Ludwigia pilosa* is, however, usually hirtellous around the style base and between the disc lobes. Plants of *L. sphaerocarpa* are sometimes hirtellous between the disc lobes, too. In densely strigillose populations of *L. linearis*, the nectary discs tend to be strigillose throughout or between the lobes also. In *L. linifolia* and *L. stricta*, the disc lobes are minutely papillose throughout, as are their fruit and seed surfaces.

CAPSULES

Characters of the capsules have been very useful to systematic and phylogenetic studies in *Ludwigia* (Small, 1933; Munz, 1942, 1944; Raven, 1963; Eyde, 1978; Ramamoorthy & Zardini, 1987). When Small (1933) first grouped plants of *Ludwigia* sect. *Microcarpium* (as "Microcarpeae"), the mode of capsular dehiscence was one of the main criteria. Although his observations on capsular dehiscence were incomplete and not all species in this group have capsules dehiscing by the separation of flaps from the top of the nectary disc (see below), his concept was taken up by Munz (1944, 1965) who formally described and established sect. *Microcarpium*.

The shape, size, and pubescence of capsules are very diverse within sect. *Microcarpium* (Table 2, Figs. 1–15). Capsule shape ranges from obpyramidal to subcylindric, oblong-obovate, turbinate, or subglobose, and size ranges from 1 mm long in *Ludwigia microcarpa* to 12 mm long in *L. linearis* and *L. linifolia*. The surface vestiture ranges from glabrous to minutely papillose, strigillose, or hirtellous. These characters have been extremely useful for identifying species and natural hybrids.

Furthermore, in *Ludwigia* sect. *Microcarpium*, three patterns of capsular dehiscence are recognized (Peng & Tobe, 1987), each of which has a distinct anatomical basis:

Ring dehiscence. The capsule dehisces along an apical "ring" as a result of the disintegration of thin-walled cells located between the nectary disc and the sepal base (Fig. 16). This pattern is exhibited by *Ludwigia alata*, *L. lanceolata*, *L. linearis*, *L. microcarpa*, and *L. suffruticosa*. It was previously thought of as the only way capsules of *Ludwigia* sect. *Microcarpium* dehisced (Small, 1933; Munz, 1944; Raven, 1963). In these plants

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the zonation pattern in the capsule wall is relatively simple, consisting of the outer, enlarged parenchymatous exocarp and the inner spongy endocarp.

Peeled dehiscence. The capsule dehisces by the irregular rupture of the outer capsule wall (Fig. 17). This is exhibited by *Ludwigia glandulosa*, *L. linifolia*, *L. pilosa*, *L. polycarpa*, *L. ravenii*, *L. sphaerocarpa*, and *L. stricta*. These plants have a spongy mesocarp and an endocarp with conspicuous inner hypodermis. When the seeds are dispersed, they often carry along many hypodermal cells. Whether these cells are useful for the seeds to float awaits confirmation.

Loculicidal dehiscence. The capsule dehisces by initially forming four longitudinally lenticular slits opposite each of the loculi (Fig. 18). Eventually the capsule is split into four basally united parts. This type of dehiscence is seen only in the closely related polyploids *Ludwigia curtissii* and *L. simpsonii*. In these species, the zonation pattern of the fruit wall is basically similar to that of the "ring-dehiscent" species, except that the exocarp consists only of the outer epidermis and a single-celled layer of outer hypodermis compactly aligned beneath. These hypodermal cells are remarkably enlarged and radially elongate except along the median longitudinal line facing each locule, where they are abruptly reduced or replaced by small, parenchyma cells. It is exactly along these four lines that the capsules dehisce at maturity.

To summarize, the fruit wall of all species of *Ludwigia* sect. *Microcarpium* is differentiated into a spongy zone (endocarp in ring-dehiscent and loculicidally dehiscent species, or mesocarp in peeled-dehiscent species) and a continuous zone. As Eyde (1978) suggested, such differentiation undoubtedly aids seed dispersal by reducing the effective thickness and by the differential growth rate that could result in the separation of the outer layers from the inner. The specialized hypodermis in *L. curtissii* and *L. simpsonii* appears to represent a condition that has evolved a step beyond this point.

SEEDS

In all species of sect. *Microcarpium*, seeds have a narrow raphe and are free and pluriseriate in each locule of the capsule, with a narrow raphe. The seeds are small, from 0.4 to 0.7 mm long, and are cylindric, ellipsoid, reniform, or ovoid. They are mostly yellowish, light brown, or brown in color, although three species, *Ludwigia linifolia*, *L. microcarpa*, and *L. stricta*, nearly always have dark reddish seeds.

Eyde (1978) was the first to point out that species of sect. *Microcarpium* are remarkably diverse in surface cell orientation. Like capsule morphology, or rather together with capsule morphology, seed surface pattern provides excellent diagnostic characters for identifying the species and detecting natural hybrids. The seed surface cells are either subisodiametric or are elongate parallel or elongate transversely to the seed length, with minor variation on the two ends and areas near the raphe (Figs. 19–34). Although in different populations of both *L. glandulosa* and *L. linearis* the seed surface cells are oriented in two different ways, the pattern is not random. In *L. glandulosa*, the cells are elongate parallel to the seed length in subsp. *glandulosa* (Fig. 23) and transversely elongate in the western, short-fruited subsp. *brachycarpa* (Fig. 24). Plants of *L. linearis* are extremely variable in pubescence, ranging from completely glabrous to densely strigillose. In general, seed surface pattern seems to be correlated with pubescence: subglabrous plants usually exhibit cells elongate parallel to the seed length (Fig. 21), whereas densely strigillose individuals generally have seed surface cells elongate transversely to the seed length (Fig. 22).

In *Ludwigia sphaerocarpa* the seed surface cells (Fig. 29) are not as regularly oriented as they are in the other species. They are arranged in columns both transversely elongate and parallel to the seed length, with the former alignment often dominant in the central part of the seed. Some

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FIGURES 19–34. Photographs of seeds of *Ludwigia* sect. *Microcarpium*.—19. *L. linifolia*, Florida, *Dille 408* (MO).—20. *L. stricta*, Cuba, Prov. Piñar del Río, *Britton et al. 6613* (NY).—21. *L. linearis*, North Carolina, Chatham Co., *Campbell 1077* (NCU).—22. *L. linearis*, Louisiana, St. Tammany Parish, *Dille 420* (MO).—23. *L. glandulosa* subsp. *glandulosa*, Florida, Santa Rosa Co., *Dille 412* (MO).—24. *L. glandulosa* subsp. *brachycarpa*, Louisiana, Cameron Parish, *Peng 4367* (MO).—25. *L. polycarpa*, Missouri, Lincoln Co., *Dille 443* (MO).—26. *L. suffruticosa*, Florida, Hillsborough Co., *Peng 4327* (MO).—27. *L. lanceolata*, Florida, Highlands Co., *Peng 4183* (MO).—28. *L. alata*, Florida, Wakulla Co., *Morar 11* (FSU).—29. *L. sphaerocarpa*, South Carolina, Jasper Co., *Dille 348* (MO).—30. *L. pilosa*, Georgia, Emanuel Co., *Peng 4025* (MO).—31. *L. ravenii*, North Carolina, Sampson Co., *Boufford & Wood 18898* (MO).—32. *L. microcarpa*, Florida, Collier Co., *Peng 4281* (MO).—33. *L. simpsonii*, Florida, Collier Co., *Peng 4266* (MO).—34. *L. curtissii*, Florida, Collier Co., *Peng 4357* (MO). Scale bar = 0.5 mm, except in Figure 25; there scale bar = 0.4 mm.

seeds of this species have variously oriented cells, a pattern that supports the suggestion of a hybrid origin for *L. sphaerocarpa* (see below).

Reproductive Biology

All 14 species in *Ludwigia* sect. *Microcarpium* are genetically self-compatible perennials that reproduce sexually and vegetatively. About two-thirds of them are modally autogamous—a statistic comparable to that for the whole genus (Raven, 1979). Shortly after the flowers open in the morning, the stigma becomes sticky and receptive and the stamens dehisce, exposing yellowish pollen entangled by the viscin threads. Initially the stamens are held away from the stigma and spread apart. The filaments, however, gradually arch toward the center and finally the anthers become firmly appressed to the sides of the sticky stigma in one to several hours (usually before noon), thus effecting self-pollination. This occurs in petaliferous as well as apetalous species, with the exceptions discussed in the following paragraph.

In *Ludwigia alata*, *L. pilosa*, *L. suffruticosa*, and many individuals of *L. sphaerocarpa*, the anthers also bend toward the stigma at late anthesis, but the distance between the androecium and the gynoecium is such that self-pollination is impossible without the intervention of a pollen vector. In the first three, apetalous, species the sepals are conspicuous and creamy within; in *L. pilosa* they are often tinged with pink along the main veins and the edges. Presumably these petaloid sepals serve to attract insect pollinators. In addition, these three species have yellowish discs that produce abundant nectar. *Ludwigia sphaerocarpa*, by contrast, has sepals that are yellowish within and very bright yellow discs that are more conspicuous than those of any other species, with the possible exception of *L. linifolia* (see below). Outcrossing in all four above-mentioned species is therefore not reinforced by protogyny/protandry or by male sterility, but merely by the physical separation of the stigma and the anthers. The self-incompatibility found in the more primitive members of *Ludwigia* sect. *Myrtocarpus* sensu lato is not present in sect. *Microcarpium*.

Nectary discs are present in all species in sect. *Microcarpium*, but they vary in size and in the quantity of nectar produced. *Ludwigia microcarpa*, an apetalous species with tiny flowers (the ovary is less than 1 mm long), has a nearly flat, greenish disc that produces very little nectar, and is presumably highly autogamous. Despite this, the fact that several natural hybrids—e.g., *L. microcarpa* × *L. curtissii* and *L. microcarpa* × *L. simpsonii*, and an intersectional hybrid, *L. microcarpa* × *L. palustris* ($n = 8$; sect. *Dantia*)—were collected in the field where the parental species grow sympatrically (see below) suggests that insect pollinators do occasionally visit plants with minute, inconspicuous flowers.

Living plants from two of the three petaliferous species were available for observation; *Ludwigia stricta*, endemic in Cuba, has not been studied as a living plant. Flowers of *L. linifolia* have very conspicuous nectary discs that produce copious nectar. This, along with the yellow petals, serves to make the flowers highly attractive to insects. *Ludwigia linearis* has a comparatively shallow ovary disc that secretes less nectar. This species is noteworthy in sharing with the unrelated South American *L. latifolia* (Benth.) Hara (sect. *Tectiflora*) the distinction of being the only members of the genus *Ludwigia* in which the sporogenous tissue of the anthers is divided into packets horizontally by both tapetum and parenchyma (Eyde, 1977; Tobe & Raven, 1986). This character is also shared by five other genera of Onagraceae, as mentioned previously.

Paper wasps of the genus *Polistes* have been observed to visit flowers of species of *Ludwigia* sect. *Microcarpium* grown in the netted experimental greenhouse at the Missouri Botanical Garden. In the field, more insects (usually bumblebees, honeybees, and wasps) were attracted to *L. pilosa* and, less so, to *L. sphaerocarpa*. Moths and ants have also been observed visiting *L. pilosa*. Relatively few field observations of insect pollinations on other species have been made in my trips to the southeastern United States. Circumstantial evidence from the presence of abundant natural hybrid populations suggests that insect pollination must be more common than I have observed.

In addition to sexual reproduction, nearly all species of *Ludwigia* sect. *Microcarpium* produce sprawling stolons at the base of the erect, flowering stems late in their flowering season. This vegetative reproduction enables the plants to overwinter, when the erect stems die back; in spring, they can then produce a large colony before other species can invade. Some of the sterile populations of natural hybrids also persist by this means. In *L. suffruticosa*, however, stolons are not as common as underground rhizomes. In *L. curtissii* and *L. simpsonii*, stolons are not apparent. These plants simply form new shoots from the lower nodes of the died-back stem of the previous year. These shoots are decumbent or ascending initially, but soon become erect.

Cytology

Chromosomes of *Ludwigia* are the smallest in the Onagraceae, and they may differ conspicuously in size within a single genome. The proximal ends of the chromosomes are heavily pycnotic and appear in interphase nuclei as very distinct and definite chromocenters (Kurabayashi et al., 1962). The basic chromosome number of the genus is $x = 8$, with no aneuploidy but extensive polyploidy (Raven & Tai, 1979). Through the efforts of Gregory & Klein (1960), Kurabayashi et al. (1962), Raven & Tai (1979), and Peng (1984, 1988), the chromosome numbers of all species of *Ludwigia* sect. *Microcarpium* have been established. There are four diploid species with $n = 8$ (*L. linearis*, *L. linifolia*, *L. microcarpa*, and *L. stricta*), eight tetraploid taxa with $n = 16$ (*L. glandulosa* subsp. *glandulosa*, *L. glandulosa* subsp. *brachycarpa*, *L. lanceolata*, *L. pilosa*, *L. polycarpa*, *L. ravenii*, *L. sphaerocarpa*, and *L. suffruticosa*), two hexaploid members with $n = 24$ (*L. alata* and *L. simpsonii*), and an octoploid with $n = 32$ (*L. curtissii*). For a review and discussions see Peng (1988).

Ecology and Geographical Distribution

With the exceptions of *Ludwigia stricta*, which is endemic to Cuba, and *L. polycarpa*, which is distributed mainly in the northcentral United States, *Ludwigia* sect. *Microcarpium* is confined primarily to the Coastal Plain of the southeastern United States. Several species also extend further south or east: *L. alata* to Jamaica; *L. curtissii* to the Bahamas; and *L. linifolia* disjunct to Tabasco, Mexico. *Ludwigia simpsonii* occurs in Cuba and Jamaica, and *L. microcarpa* in the Bahamas, Cuba, and Jamaica. *Ludwigia stricta* is exceptional in being endemic to Cuba. A detailed description of the ranges with maps for each species is given in the taxonomic treatment.

Like *Ludwigia* species occurring in other parts of the world, plants of *Ludwigia* sect. *Microcarpium* grow in wet habitats. They are commonly found along alluvial ground or in the shallow water of many areas, including ponds, lakes, rivers, streams, lagoons, sloughs, backwaters, swales, wet meadows or prairies, open swamp forests, drainages, and irrigation ditches. All species grow in sandy or occasionally peaty soils. A few species grow in brackish marsh or tidal flats (*L. alata*, *L. linifolia*, *L. microcarpa*, and *L. simpsonii*), in sinks in limestone prairies (*L. alata*, *L. curtissii*, *L. microcarpa*, *L. simpsonii*, *L. sphaerocarpa*, and *L. suffruticosa*), and in clay soils (both subspecies of *L. glandulosa*). None of the species in *Ludwigia* sect. *Microcarpium* exhibit the aggressiveness characteristic of weedy plants, although the following taxa have rarely been observed growing in disturbed habitats: *L. linearis*, *L. microcarpa*, *L. simpsonii*, and both subspecies of *L. glandulosa*.

Experimental Hybridization

Results from the extensive artificial hybridization among members of *Ludwigia* sect. *Microcarpium* (Peng, 1988) are summarized as follows.

1. There is generally little difficulty in obtaining hybrids between members of sect. *Microcarpium*; most F_1 plants grow to maturity, and many set abundant seeds. Hybrids between plants of the same ploidy level are generally intermediate in morphology; hybrids between plants of different ploidy levels tend to be more similar to the parent with the higher chromosome number. Character such as capsule shape and size, bracteole length, overall pubescence, presence or absence of petals, seed surface pattern, and pollen stainability are very useful in distinguishing species and identifying hybrids.
2. All diploid species can be crossed with one another and form floriferous F_1 plants. Hybrids between the petaliferous diploids with narrow leaves (*Ludwigia linearis* and *L. linifolia*) are vigorous, have ca. 50% stainable pollen, and produce a moderate amount of viable seeds. A modal meiotic configuration of a ring or chain of four plus six bivalents are frequently observed in reciprocal F_1 hybrids. Hybrids between either of the petaliferous diploids and the apetalous, diploid *L. microcarpa* are, in contrast, highly sterile as to pollen and seed set. Nearly all chromosomes remain unpaired in meiosis in these hybrids.
3. All eight tetraploid members studied are interfertile: chromosome pairing in meiosis is nearly complete, and pollen stainability and seed set are high in hybrids between any two tetraploid species, no matter how different they are from each other morphologically.
4. Although the two hexaploid ($n = 24$) species, *Ludwigia alata* and *L. simpsonii*, can be crossed and produce healthy F_1s, meiosis is irregular with abundant unpaired chromosomes. The affinity of *L. alata* is apparently with species of the tetraploid group, based on morphological characters. Hybrids between *L. alata* and any tetraploid species are easily obtained. They produce moderate seed set and have 43–71% stainable pollen. Meiosis in these F_1 individuals

typically exhibited a maximum of 16 bivalents and eight unpaired chromosomes. By contrast, the hexaploid *Ludwigia simpsonii* ($n = 24$) is clearly allied to the octoploid *L. curtissii* ($n = 32$). Hybrids between them are highly fertile, having 80–90% stainable pollen and producing good seed set. These plants consistently exhibited a meiotic configuration of 24 bivalents and eight unpaired chromosomes.

5. Seeds obtained from crossing species of any two of the following groups, (1) tetraploid species group (including the allied *Ludwigia alata*), (2) diploid species, and (3) *L. curtissii* and *L. simpsonii*, often failed to germinate. Those that germinate may either be inviable or produce flowers that set negligible or no seed and tend to have very low levels of stainable pollen. For a complete discussion of the experimental hybrids, consult Peng (1988).

Natural Hybridization

Experimental hybridization (Peng, 1988) revealed that vigorous and floriferous hybrids can readily be obtained between most members of *Ludwigia* sect. *Microcarpium*. The general lack of postzygotic barriers and the facts that all species in this section are perennial and that most of them are sympatric, have similar preference for habitats, flower in the morning during the same season, are facultatively outcrossing, and have similar kinds of indiscriminate insect pollinators, strongly suggest that natural hybrids should be fairly common in the field.

Field observations and herbarium study show that hybrid populations of *Ludwigia* sect. *Microcarpium* are indeed abundant. Except for this and the companion paper (Peng, 1988), however, very little has been reported about the natural hybrid populations of sect. *Microcarpium*. The variation patterns generated by the intergradation among some members of sect. *Microcarpium* have previously been detected by Torrey & Gray (1840) and Small (1903); such plants were given names at varietal and specific rank respectively, but no indication of their hybrid origins was mentioned. Torrey & Gray (1840) described *L. capitata β pubens* from a population of *L. suffruticosa* × *L. pilosa* from Georgia; Small (1903) applied the name *L. simulata* to a population of *L. pilosa* × *L. lanceolata* from North Carolina.

Duke (1955) was the first to point out that some *Ludwigia* species show varying degrees and patterns of intergradation in North Carolina. In his informative study, he compared the morphological characters of a mixed population consisting of plants of *L. pilosa*, *L. glandulosa*, and the intermediates, and considered the latter as possible hybrids. Upon examination of his voucher collections, it is confirmed beyond doubt that these plants represent uniform F_1 hybrids of *L. pilosa* × *L. glandulosa*. Duke (1955) further suggested that "self-pollination is the rule in this genus, and that cross-pollination is a very rare exception to the rule," and speculated that phyllophagous insect caterpillars may have brought about cross-pollination while foraging leaves. This, however, is not true, as at least four species in sect. *Microcarpium* have somewhat showy sepals and produce copious nectar and require insect vectors to pollinate their flowers to set seeds. Such insects as bumblebees, wasps, honeybees, moths, and even ants have frequently been seen obtaining nectar on the flowers of *Ludwigia* sect. *Microcarpium*.

In a biosystematic study of *Ludwigia* sect. *Dantia*, a close ally of sect. *Microcarpium* with opposite leaves and prostrate habit, Schmidt (1967) reported two intersectional hybrids, *L. repens* × *L. simpsonii* (as *L. repens* × *L. curtissii*) and *L. palustris* × *L. glandulosa* from North Carolina and Florida, respectively. His observations of the hybrid between *L. palustris* ($n = 8$; sect. *Dantia*) and *L. glandulosa* ($n = 16$; sect. *Microcarpium*) revealed very little association between chromosomes, with 0–3 weakly joined bivalents in meiosis. The other natural hybrid, involving *L. repens* ($n = 24$; sect. *Dantia*) and *L. simpsonii* ($n = 24$; sect. *Microcarpium*), yielded 48 unpaired chromosomes at mesiosis, suggesting the dissimilarity in the genomes of plants in the two North American sections.

Observation of individuals exhibiting a combination of characters intermediate between distinct taxa initially suggests natural hybridization. Members of the following species pairs, *Ludwigia alata* ($n = 24$) and *L. lanceolata* ($n = 16$), *L. pilosa* ($n = 16$) and *L. ravenii* ($n = 16$), and *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$), however, are usually so similar in appearance, especially in dried herbarium specimens, that their hybrids cannot be recognized readily.

Results from experimental hybridization suggest that capsule shape and size are the most important diagnostic characters for detecting hybrids in sect. *Microcarpium*. Other useful features include overall pubescence, seed surface cell shape and orientation, the presence or absence of petals, whether pollen grains are shed singly vs. in tetrads, and pollen stainability. Seed surface pattern is useful only for the determination of hybrids in the tet-

raploid group (including *Ludwigia alata*), as these nine taxa are interfertile, yield abundant seeds, and are diverse with respect to this character. Absence of developing fruits and low levels of pollen stainability, however, are characteristic of hybrids resulting from all other heteroploid crosses, with the exception of *L. curtissii* ($n = 32$) × *L. simpsonii* ($n = 24$). As a last resort, chromosome number and meiotic chromosome behavior are useful indicators of natural hybrids when the parents involved have different chromosome numbers or differentiated genomes.

The natural hybrid populations mentioned below are discussed individually following the treatment of the species in the systematic section. Full citation of these specimens of hybrids is given in the companion paper (Peng, 1988).

Field experience indicates that natural hybrid populations are fairly common wherever two or more species grow side by side. A total of 15 intrasectional hybrids and seven intersectional (among plants of sects. *Microcarpium* and *Dantia*) hybrids are recognized (Peng, 1988). Hybrids resulting from crosses among members of the tetraploid species group (including *Ludwigia alata*) are by far the most common. The following hybrid combinations are representative: *L. alata* × *L. pilosa* (four populations from Florida, one from Georgia, and one from Mississippi), *L. alata* × *L. suffruticosa* (seven populations from Florida), *L. glandulosa* subsp. *glandulosa* × *L. glandulosa* subsp. *brachycarpa* (one from Oklahoma and one from Texas), *L. glandulosa* subsp. *glandulosa* × *L. pilosa* (two from North Carolina, one from Georgia, one from Alabama, and two from Mississippi), *L. glandulosa* subsp. *glandulosa* × *L. sphaerocarpa* (one from South Carolina, one from Missouri), *L. lanceolata* × *L. pilosa* (three populations from Florida), *L. lanceolata* × *L. suffruticosa* (two from Florida), *L. pilosa* × *L. sphaerocarpa* (many populations from North Carolina, South Carolina, Georgia, Florida, Alabama, and Texas), *L. pilosa* × *L. suffruticosa* (two from North Carolina, three from Georgia, and two from Florida), and *L. polycarpa* × *L. sphaerocarpa* (two populations from Indiana). Backcrossed generations or segregates of advanced generations are found of *L. lanceolata* × *L. suffruticosa*, *L. pilosa* × *L. suffruticosa*, and most abundantly of *L. pilosa* × *L. sphaerocarpa*.

As in the case of artificial hybridization, the tetraploid hybrids are highly fertile as to seed and pollen; hybrids between the hexaploid *Ludwigia alata* and the tetraploid species have slightly lower levels of stainable pollen and seed set. It is noteworthy that in nearly all of the above hybrids at least one member of each pair of putative parents is unable to undergo mechanical self-pollination and has somewhat showy sepals. In other words, *L. alata*, *L. pilosa*, *L. sphaerocarpa*, and *L. suffruticosa* hybridize more frequently than other tetraploid species that are modally autogamous.

Sporadic occurrence of sterile triploid hybrids include *Ludwigia glandulosa* ($n = 16$) × *L. linearis* ($n = 8$) (one population from North Carolina and the other from Georgia) and *L. sphaerocarpa* ($n = 16$) × *L. linearis* (one population from Alabama). One probably diploid hybrid population of *L. linearis* × *L. linifolia* was collected from Florida in 1981. Attempts to re-collect and to study live plants of this hybrid have failed, because the habitat was destroyed (Popenoe, pers. comm.).

Hybrids between *Ludwigia curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$) very probably occur in the field but would be difficult to detect. *Ludwigia curtissii* hybridizes with *L. linifolia* ($n = 8$) and with *L. microcarpa* ($n = 8$) to form sterile hybrids. At least four populations of *L. simpsonii* × *L. microcarpa* are known from Florida. It is of interest to note that among the putative parental species here concerned, only *L. linifolia* has somewhat showy petals and produces copious nectar, whereas all other species are probably modally autogamous.

Hybrids involving putative parents from sect. *Microcarpium* and sect. *Dantia* are also not uncommon. *Ludwigia repens* ($n = 24$; sect. *Dantia*) hybridizes with *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$) in Florida. At least eight such populations are known, all producing flowers, but the ovaries abort after mechanical self-pollination. *Ludwigia palustris* ($n = 8$; sect. *Dantia*), a widespread and apparently autogamous species, hybridizes with *L. glandulosa* subsp. *glandulosa* ($n = 16$) and forms sterile hybrid populations in Virginia (one population). It also hybridizes with the diploid, small-flowered and presumably autogamous *L. microcarpa* of sect. *Microcarpium* and forms sterile hybrids in North Carolina (one population), Georgia (one population), and Florida (three populations). In Kentucky, *L. palustris* hybridizes with *L. polycarpa* ($n = 16$) and likewise forms sterile hybrids.

The only intersectional tetraploid hybrid is known from a single population of *Ludwigia arcuata* ($n = 16$; sect. *Dantia*) × *L. pilosa* ($n = 16$) collected from Alabama. Flowers of both putative parents are showy and attract many insect pollinators. Established hybrids, however, are very rare in nature. Although some seeds were observed in mature cap-

TABLE 3. Comparison of diploid petaliferous species in *Ludwigia* sect. *Microcarpium*.

Characters	*L. linearis*	*L. linifolia*	*L. stricta*
Plant height (cm)	(22–)50–100(–145)	12–55(–62)	10–60(–85)
Cauline leaves	Very narrowly elliptic to sublinear	Oblanceolate-linear to linear	Oblanceolate or elliptic to narrowly so
Abaxial marginal veins	Distinct	Obscure	Obscure
Sepal			
Length (mm)	2.3–5(–5.6)	(3.3–)4–7	(1.8–)2–3
Width (mm)	1–3(–3.5)	1.1–1.7	0.9–1.5
Length : width	1.5–2.5	3–4	2
Anther length (mm)	1–2	0.65–1.1	0.5–0.7
Septa in anther sac	Present	Lacking	Lacking
Filament length (mm)	1.1–2(–2.2)	(1.3–)1.5–2.5(–3)	0.75–1.1
Style length (mm)	(0.4–)0.7–1.5	1.25–2.5	0.55–0.9
Stigma			
Shape	Cylindric	Depressed globose	Depressed globose
Length	(0.6–)1–1.9	0.3–0.6	0.25–0.5
Nectary disc	Shallow	Very prominent	Prominent
Capsule			
Shape	Elongate-obpyramidal	Subcylindrical	Subcylindrical
Surface	With a shallow, longitudinal groove on each side	Nearly smooth	Nearly smooth
Length (mm)	5–10(–12)	5–10(–12)	5–6(–7)
Thickness (mm)	2–5.5	1.3–2(–2.2)	1.6–1.8
Dehiscence	Ring-dehiscent from top	Peeling off from the sides	Peeling off from the sides
Bracteole length (mm)	0.4–4(–7.5)	(1.5–)2.5–9(–13)	0.7–2.5(–3)
Seed			
Color	Yellowish	Reddish brown	Reddish brown
Surface cell shape	Columnar	Subisodiametric	Subisodiametric

sules of the herbarium specimen (Mobile Co.: Audubon Bird Sanctuary, Dauphin Island, *Deramus 0643* [DS, UNA]), they are probably inviable. Such hybrids synthesized in the experimental greenhouse showed a remarkably high level of chromosome pairing (ca. 12–15 bivalents and 2–8 unpaired univalents; 1 or 2 trivalents occasionally seen) but had only 38% stainable pollen. Not a single seed was set despite many attempts at artificial self-pollination (like *L. pilosa*, this hybrid cannot undergo mechanical self-pollination).

To summarize, geographical isolation and self-pollination are the primary factors limiting natural hybridization among species of *Ludwigia* sect. *Microcarpium*. For example, *L. polycarpa* occurs in the central Midwest (Fig. 45), where it is isolated geographically from all other species of sect. *Microcarpium* except *L. sphaerocarpa*. Where the two species come into contact, hybridization occurs. *Ludwigia microcarpa*, an extreme selfer, has been hybridized successfully with most species of sect. *Microcarpium* in the greenhouse, and the resulting hybrids were vigorous. *Ludwigia microcarpa* grows sympatrically with many other species, but natural hybrids have been found only with *L. simpsonii*, *L. curtissii*, and some members of sect. *Dantia*.

In general, natural hybrids are usually frequent wherever two species occur together. This is particularly true for plants in the tetraploid group, hybrids of which were often found intermixed with putative parents. The sorts of disturbed habitats suggested by Anderson (1948) do not appear to be necessary for the establishment of natural hybrids in *Ludwigia* sect. *Microcarpium*.

As outlined above, natural hybridization is not limited to species within *Ludwigia* sect. *Microcarpium*. At least seven hybrid combinations, some of which occur commonly in nature, have been found between members of sect. *Microcarpium* and sect. *Dantia*. Most of these have also been synthesized in the experimental greenhouse. None

of the intersectional hybrids set viable seeds, although they are usually very vigorous and appear to compete well with their parents. Once established, these sterile hybrids may be able to persist in a given location due to their perennial habit. Furthermore, new colonies may be established vegetatively if entire plants or fragments are transported to suitable habitats, most likely by water.

Evolutionary Relationships

Ludwigia sect. *Microcarpium* consists of four diploids, eight tetraploids, two hexaploids, and one octoploid.

Ludwigia microcarpa is distinct among the diploid species by the more or less spatulate cauline leaves and small, inconspicuous, apetalous flowers; and it is modally self-pollinated. All three other diploid species, *L. linearis*, *L. linifolius*, and *L. stricta*, have elongate, narrow leaves and relatively showy, petaliferous flowers and are facultatively outcrossing. The divergence of *L. microcarpa* from the rest of the diploids is further demonstrated by the cytogenetic study of artificial hybrids in this group. Artificial F_1 hybrids between *L. microcarpa* and either *L. linearis* or *L. linifolia* were completely sterile; in meiosis they revealed very few chromosome associations, with 0–3 weakly joined bivalents.

Ludwigia linearis is unusual in sharing with the unrelated South American species *L. latifolia* (Benth.) Hara (sect. *Tectiflora*) the character of polysporangiate anthers in which the locules are divided by transverse septa composed of tapetum and parenchyma. Otherwise, *L. linearis* is apparently somewhat related to *L. linifolia*. The two species differ chromosomally by at least one reciprocal translocation. F_1 hybrids between them have ca. 50% stainable pollen, and they produce moderate quantities of viable seeds.

Ludwigia stricta, which is endemic to Cuba, is more closely related to *L. linifolia* than to any other species in sect. *Microcarpium*. It differs from *L. linifolia* only by the broader leaves, smaller floral parts, and shorter fruits (Table 3). The crossing relationships of *L. stricta* with other diploid species are currently being investigated.

The eight tetraploid taxa ($n = 16$) are uniformly apetalous and are otherwise remarkably diverse in overall pubescence, shape and color of sepals, shape and dehiscence of capsules, bracteole length, seed surface cell pattern, and whether pollen is shed singly or as tetrads. Correlations in these features, however, are evidently nonexistent. It is therefore of great interest to find that these eight morphologically well-delimited taxa can be crossed in any combination and produce vigorous and fertile offspring. The hybrids exhibit nearly complete chromosome pairing and high levels of stainable pollen. Natural hybridization among plants of this group is abundant, especially among those members with somewhat showy sepals. Most natural hybrids are F_1 plants that occur in more or less undisturbed habitats where the putative parents also grow. Introgressed populations or segregates of advanced generation of *Ludwigia pilosa* × *L. sphaerocarpa* hybrids, however, are also abundant and widespread. Cytogenetic studies of experimental hybrids between the tetraploid species and the diploid species suggest that no extant diploids are believed to have been involved directly in the formation of the tetraploid species group.

Ludwigia alata, a hexaploid ($n = 24$) species, resembles the tetraploids morphologically. Superficially it is most similar to *L. lanceolata* in general aspect and especially in the characters of winged capsules. Nearly all of the reciprocal hybrids between the hexaploid *L. alata* and any of the tetraploid species exhibited a modal meiotic configuration of 16 bivalents and 8 univalents, which suggests that they share two genomes in common. Judged from the morphology of the hexaploid and from the pairing of chromosomes in experimental hybrids, *L. alata* probably originated following hybridization between one of the tetraploids, perhaps *L. lanceolata*, and the diploid *L. microcarpa*, or populations ancestral to them.

The affinity of the other hexaploid, *Ludwigia simpsonii*, however, is definitely with *L. curtissii*, the only octoploid in sect. *Microcarpium*. These two species are unique in having loculicidal capsules and in having, along with the diploid *L. microcarpa*, more or less spatulate cauline leaves. *Ludwigia curtissii* and *L. simpsonii* are polymorphic and are sometimes difficult to distinguish morphologically. Cytogenetic data suggest that the hexaploid chromosome complement of *L. simpsonii* includes three different genomes, one of which is identical with that of *L. microcarpa*. Artificial hybrids between *L. simpsonii* and *L. curtissii* exhibited a meiotic configuration of 24 bivalents and eight univalents, which suggests that these two closely related species possess three genomes in common. Based on morphological characters and crossing relationships, the octoploid *L. curtissii* was probably derived following hybridization between a petaliferous, narrow-leaved diploid lineage similar to *L. linifolia* and the hexaploid *L. simpsonii*.

To summarize, following the differentiation of diploid species of *Ludwigia* sect. *Microcarpium*, some diploids have evidently become extinct. Natural hybridization among the diploid lineages fol-

lowed by polyploidy has played a major role in the evolution of this group. Postzygotic genetic barriers do not separate most of the species of this section. Rather, the major limiting factor to natural hybridization appears to be the modally autogamous breeding system of most species. Geographical isolation is important only with respect to *L. polycarpa*, which is distributed well to the north of nearly all the other taxa.

Natural hybridization is prevalent within *Ludwigia* sect. *Microcarpium*, and hybrids often grow intermixed with putative parental populations. All interploid hybrids are completely sterile except for crosses between *L. alata* ($n = 24$) and the tetraploid species ($n = 16$), and crosses between *L. curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$). Even sterile hybrids, however, can persist and form large colonies, at least locally, by means of strong vegetative reproduction via stolons.

Natural hybrids are especially common among members of the tetraploid group (including *Ludwigia alata*) and are nearly always vigorous and fertile. Especially complex is the pattern of variation in the tetraploid *L. sphaerocarpa*, which is apparently comprised largely of widespread stabilized hybrid populations that exhibit a combination of characters distinguishing them from other taxa. As in the evolution of *Epilobium* in New Zealand (Raven & Raven, 1976), the recombination of genetic information from somewhat differentiated populations followed by the maintenance of well adapted genetic strains by a combination of autogamy and vegetative reproduction appears to have played a central role in the evolution of the polyploid members of *Ludwigia* sect. *Microcarpium*.

Systematic Treatment

Ludwigia sect. **Microcarpium** Munz, Bull. Torrey Bot. Club 71: 154. 1944; N. Am. Fl. ser. II, pt. 5: 42. 1965. Raven, Reinwardtia 6: 336. 1963. "*Microcarpeae*" Small, Man. S.E. Fl. 941. 1933. Type species: *Ludwigia pilosa* Walter.

Erect perennial herbs, perennating mostly by leafy, basal stolons (mainly by rhizomes in *Ludwigia suffruticosa*). Stems usually profusely branched except in *L. suffruticosa*, becoming swollen and spongy below when submerged. Leaves alternate, sessile or nearly so, subentire, usually with hydathodal glands along margins. Flowers sessile or shortly pedicellate, axillary (in very compact, short racemes or spikes in *L. suffruticosa*). Bracteoles in subopposite pairs attached from the base of the pedicel to halfway up the ovary. Flowers 4-merous, mostly apetalous (consistently with 4 petals in 3 diploid species). Sepals mostly greenish (creamy white or yellowish in 4 apetalous species). Stamens haplostemonous; anther sacs undivided except in *L. linearis*, in which the polysporangiate anthers are partitioned horizontally by tapetums and parenchyma. Pollen shed singly or as tetrads. Nectary disc 4-lobed, usually shallowly raised above ovary apex (flat in *L. microcarpa*). Capsules with ca. 10–700 seeds, obpyramidal to subcylindric, oblong-obovoid, turbinate, or subglobose, dehiscent by the separation of the disc and the ovary wall, or forming 4 longitudinally lenticular slits opposite each locule, or the irregular rupture of the outer wall. Seeds yellowish, light tan to reddish brown, free and pluriseriate in each locule, with a narrow raphe; surface cells suborbicular, elongate parallel to or perpendicular to the seed length. Self-compatible, modally autogamous in most species. Gametic chromosome number, $n = 8, 16, 24, 32$.

Distribution. Atlantic and Gulf Coastal Plain of the United States (*Ludwigia polycarpa* is exceptional by ranging into the northcentral United States), Bahamas, Cuba, Jamaica, and Tabasco, Mexico.

Key to the Species of *Ludwigia* sect. *Microcarpium*

1a. Capsules elongate, at least twice as long as broad.
  2a. Petals absent; leaves narrowly elliptic ..... 4. *L. glandulosa*
  2b. Petals 4; leaves sublinear to linear.
    3a. Lateral and marginal veins on abaxial leaf surface distinct; capsules elongate-obpyramidal, ring-dehiscent on top; seeds yellowish; anthers 1–2 mm long, the sacs septate ..... 3. *L. linearis*
    3b. Lateral and marginal veins on abaxial leaf surface obscure; capsules subcylindric, peeled-dehiscent from the sides; seeds reddish brown; anthers 0.5–1.1 mm long, the sacs not septate.
      4a. Sepals (3.3–)4–7 mm long, ca. 3–4 times as long as wide; filaments (1.3–)1.5–3 mm long; style 1.25–2.5 mm long; bracteoles (1.5–)2.5–13 mm long; U.S. & Tabasco, Mexico ..... 1. *L. linifolia*
      4b. Sepals 1.8–3 mm long, 2 times as long as wide; filaments 0.75–1.1 mm long; style 0.55–0.9 mm long; bracteoles 0.7–2.5(–3) mm long; Cuba ..... 2. *L. stricta*
1b. Capsules various, less than twice as long as broad.
  5a. Flowers in compact racemes or spikes 1–5 cm long; stems single or with a few branches frequently overtopping the main stem; rhizomes often present ..... 6. *L. suffruticosa*

5b. Flowers axillary, in elongate, interrupted, leafy racemes or spikes 2–20 cm long; stems usually profusely branched; rhizomes absent.
6a. Plants densely pubescent throughout.
7a. Sepal apex elongate-acuminate or subcuspidate, reflexed; plants densely hirtellous; seed surface cells suborbicular ..... 10. *L. pilosa*
7b. Sepal apex acuminate, ascending; plants densely strigillose or hirtellous; seed surface cells columnar.
8a. Plants hirtellous; capsules oblong-obovoid; sepals greenish adaxially; bracteoles (1.5–)2–4.3 mm long, at or near capsule base ..... 11. *L. ravenii*
8b. Plants strigillose; capsules subglobose; sepals yellowish adaxially; bracteoles 0.5–1.5 mm long, usually on the short pedicel ..... 9. *L. sphaerocarpa*
6b. Plants subglabrous to glabrous.
9a. Capsules obpyramidal with narrowly winged corners.
10a. Stems nearly smooth or slightly ridged; sepals greenish, about ½ as long as the capsule; capsule wall flat between the wings; seed surface cells suborbicular; pollen grains shed as tetrads ..... 7. *L. lanceolata*
10b. Stems often distinctly ridged or winged; sepals creamy whitish, nearly as long as capsule; capsule wall between the wings bulging out longitudinally; seed surface cells elongate parallel to the seed length; pollen grains shed singly ..... 8. *L. alata*
9b. Capsules various, not winged.
11a. Nectary disc nearly flat on ovary apex; fruits 1–1.5 mm long, containing 10–20 seeds, often recognizable as bumps from outside; seeds reddish brown ..... 12. *L. microcarpa*
11b. Nectary disc distinctly raised on ovary apex; fruits 1.5–7 mm long, containing 40–500 seeds, not recognizable as bumps from outside; seeds light tan or yellowish.
12a. Cauline leaves lanceolate, oblong-elliptic to narrowly so; capsules dehiscing by irregular rupture of the outer walls; stolons present.
13a. Bracteoles 3.5–6.5(–8) mm long; sepals green, the apex elongate acuminate, reflexed; capsules oblong-obovoid with a constricted base ..... 5. *L. polycarpa*
13b. Bracteoles 0.5–1.5 mm long; sepals yellowish adaxially, the apex acuminate, ascending; capsules subglobose ..... 9. *L. sphaerocarpa*
12b. Cauline leaves obovate-spatulate, oblanceolate to very narrowly so; capsules dehiscing by 4 longitudinally lenticular slits on the wall opposite the loculi; stolons not common.
14a. Capsules 2.5–4.7 mm long; sepals 1.5–3 mm long; vestigial petals occasionally present; lower or seedling leaves always alternate ..... 14. *L. curtissii*
14b. Capsules 1.5–2.5 mm long; sepals 1.2–1.8 mm long; vestigial petals rare; lower or seedling leaves tending to be opposite or subopposite ..... 13. *L. simpsonii*

As in Figures 1–15 and 19–34, the sequence of the taxa in the taxonomic treatment reflects the possible phylogeny of *Ludwigia* sect. *Microcarpium*. Diploid petaliferous species that are presumably more primitively outcrossing are arranged first, followed by tetraploid members and the related hexaploid *L. alata*. *Ludwigia microcarpa*, an apetalous diploid, which definitely played a role in the formation of the distinct L. *curtissii* complex, is placed last along with the complex.

1. Ludwigia linifolia Poiret in Lam., Encycl. Suppl. 5: 513. 1817. *Isnardia linifolia* (Poiret) Kuntze, Rev. Gen. Pl. 1: 251. 1891. LECTOTYPE: "Amerique," *Poiret Herbarium* (P; lectotype here designated). Figure 35.

Plants glabrous. Stems erect or ascending, usually well branched, 12–55(–62) cm tall, aerenchyma rarely seen. Stolons slender, 4–15(–30) cm long, 0.7–1(–1.5) mm thick, seen in flowering season, the leaves narrowly obovate to narrowly oblanceolate, sometimes spatulate, 4.5–20 mm long, 1.3–6 mm wide, petioles 0.5–5 mm long. Cauline leaves linear or linear-oblanceolate, 15–40 mm long, (0.65–)0.9–4(–6) mm wide, the apex tapering into a sharp point or acute, margin entire with obscure hydathodal glands, the base very narrowly cuneate, sessile. Stipules narrowly ovate to narrowly lanceolate, 0.2–0.3 mm long, 0.1–0.2 mm wide. Flowers many, in leaf axils, their subtending leaves not reduced. Sepals green, narrowly triangular, ascending, (3.3–)4–7 mm long, 1.1–1.7 mm wide, glabrous or minutely papillose, the apex narrowly acute, the margin entire. Petals yellow, narrowly obovate-elliptic, 4–6 mm long, 2–4 mm wide, the apex obtuse or rounded, the base obtuse. Anthers 0.65–1.1 mm long; filaments yellowish, (1.3–)1.5–2.5(–3) mm long. Pollen shed as tetrads. Nectary disc bright yellow, elevated 0.3–0.7 mm on top of the ovary, 0.8–1.5 mm across, prominently 4-lobed, minutely papillose. Style yellow, 1.25–2.5 mm long, glabrous; stigma yellowish, 0.3–0.6 mm long, 0.6–0.8 mm thick, the apex

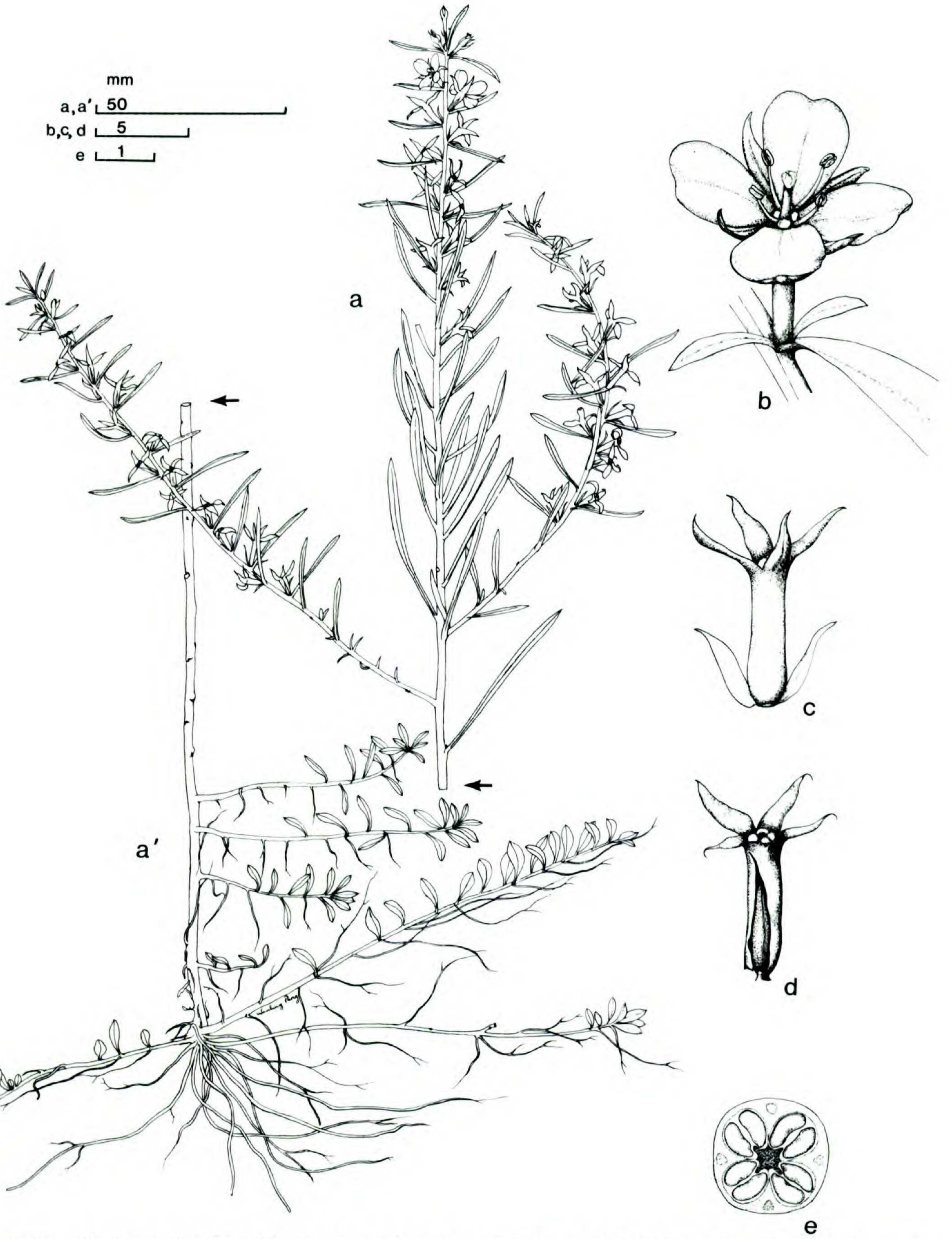

FIGURE 35. *Ludwigia linifolia*. Florida, Santa Rosa Co., *Godfrey 65936* (LL).—a. Habit, erect stem.—a′. Lower stem with basal stolons; stems continue at arrows.—b. Flower.—c. Mature capsule.—d. Dehiscent capsule.—e. Cross section of capsule.

shallowly 4-lobed. Capsules subcylindrical, slightly narrowed toward base, 5–10(–12) cm long, 1.3–2(–2.2) mm thick, densely minutely papillose, occasionally also remotely minutely scaberulous, the hairs 0.05–0.15 mm long, sessile. Bracteoles attached 0–1.5 mm above capsule base, very narrowly oblanceolate to linear, (1.5–)2.5–9(–13) mm long, 0.15–0.8 mm wide, the margin entire, ascending or spreading. Seeds reddish, oblong-elliptic with curved ends, 0.55–0.6 mm long, 0.2–0.3

FIGURE 36. Distribution of *Ludwigia linifolia* in the United States.

mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. Plants of *L. linifolia* are often found in drainage ditches, along margins of creeks or swamps, on bottom meadow, on open edges of cypress swamps, in moist pineland, and along edges of brackish lakes. *Ludwigia linifolia* ranges along the Atlantic coast from extreme southeastern North Carolina and eastern South Carolina through southern Georgia and peninsular Florida. To the west, its range extends through the Florida panhandle, to extreme southern Alabama and Mississippi. A disjunct population has been collected in north-central North Carolina (Fig. 36). It is also known from a disjunct population at Huimanguillo, Tabasco, Mexico, on the Yucatán Peninsula. Flowering from late June through October; fruiting from July through November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., 3 mi. E of Southport, *Webster & Wilbur 3559* (FSU, GH, SMU, US). Covington Co., ca. 13.5 mi. S Opp. on US 331, *Kral 32508* (DS, GA, MO, SMU, VDB). Mobile Co., W jct. ALA 188 and county 59, *Kral 37358* (FLAS, FSU, VDB). FLORIDA: Bay Co., ca. 3.4 mi. inland from Long Beach, *Godfrey & Henderson 62969* (FLAS, FSU, TEX). Bradford Co., near US 301, *Radford 8253* (NCU). Brevard Co., Okeechobee region, *Fredholm 5937* (GH, US). Calhoun Co., ca. 1 mi. NW of Blountstown, *Thorne & Davidson 16967* (FSU). Charlotte Co., Caloosa Experimental Range, U.S. Forest & Range Station, *Adams 198* (FSU). Collier Co., S of Bonita Springs, *Atwater M-78* (FLAS). DeSoto Co., Lacy, *West 171* (FLAS). Dixie Co., 4 mi. N of Suwannee, *Godfrey 56177* (FSU, GH, NY, USF). Duval Co., near Jacksonville, *Curtiss 922* (FI, FLAS, GA, GH, M, MO, NY, RB, S, US). Escambia Co., ca. 3 mi. NW Warrington, *Kral 17580* (VDB). Flagler Co., 3 mi. W of Bunnell, *Godfrey & Reinert 61115* (FSU, SMU). Franklin Co., 38.8 mi. W of jct. of US Hwys. 98 & 319, *Peng et al. 4343* (MO). Gulf Co., 3 mi. S of Port St. Joe, *Kral & Kral 7193* (FLAS, GH, USF, VDB). Hernando Co., Sections 11 & 12, T21S, R17E, *Cooley et al. 7049* (USF).

Hillsborough Co., 7 mi. NE of USF campus, *Lakela 24117* (FLAS, GH, USF). Jackson Co., 11 mi. W of Chattahoochee, *Thorne 5956* (GH). Lake Co., vicinity of Eustis, *Nash 1240* (F, GH, MO, MSU, ND, NY, US). Lee Co., Myers, *Hitchcock 119* (E, F, GH, MO, NY, US). Liberty Co., 4 mi. E Hosford, *Kral 15601* (FSU, VDB). Martin Co., Jonathan Dickinson State Park, *Popenoe 497* (FTG, NCU). Okaloosa Co., US Hwy. 98, 11.4 mi. E of Destin Bridge, *Raven 18593* (DS, FLAS, NCU, USF). Orange Co., Bog, *Fredholm 5378* (GH, US). Palm Beach Co., Corbitt Wildlife Mgmt., *Kral 5714* (FSU, SMU, VDB). Pasco Co., 1 mi. E of Gowers Corner off US 41, *Ray et al. 9934* (USF). Pinellas Co., Gulfport, *Tracy & Lloyd 225* (CM, US). St. Johns Co., 3 mi. SE of Orangedale, along FL 16, *Godfrey 70630b* (FSU, MO, NCU). St. Lucie Co., W of Walton Beach, E of US 1, *Kral 18366* (VDB). Santa Rosa Co., near Yellow River, NW of Maxton, *Godfrey 62564* (FSU, GH, SMU, VDB). Sarasota Co., along US 41, 4 mi. S of Venice, *Henderson 63-1574* (FSU, TEX). Seminole Co., near Fern Park, *Schallert 8145* (S). Wakulla Co., near Spring Creek, *Godfrey 55882* (DUKE, GH, LL, NCU, SMU, USF, VDB). Walton Co., ca. 5 mi. NE Seagrove Beach along US 98, *Kral 19360* (VDB). Washington Co., 3.5 mi. E of Caryville, *Godfrey 5962* (DUKE, FLAS, GH, NCU, VDB). GEORGIA: Baker Co., SW corner of county, *Thorne 6972* (GA). Berrien Co., 15 mi. E of Tifton, *Sargent 6686* (Herb. unknown). Bullock Co., 3.5 mi. S of Statesboro, *Bozeman 6921* (NCU). Dooly Co., 3 mi. S-SE Pitts jct., ca. 10.5 mi. S Pinehurst, *Kral 48130* (VDB). Evans Co., 5 mi. S of Claxton, *Godfrey 72098* (FSU, NCU). Glynn Co., 1.3 mi. NW of Brunswick, *Duncan 17021* (FLAS, NCU, SMU). Long Co., 5.7 mi. SE of Ludowici on GA Rt. 99, *Boole 1140* (B, NCU, SMU). McIntosh Co., NW of graveyard on Wesley Lake Rd., *Bozeman 2227* (FLAS, GA, NCU). Sumter Co., wet pine barrens, *Harper 1109* (E, GH, MO, NY, US). Ware Co., Waycross, 1900, *s.c. 4176a* (US). MISSISSIPPI: Hancock Co., US Hwy. 90, 2.5 mi. W of jct. with State Hwy. 43, *Raven 18581* (DS). Harrison Co., Gulfport, *Lloyd & Tracy 225* (NY). Jackson Co., Hwy. 90, between Orange Grove and Pecan, *Jones 14898* (FSU, GH, NY, VDB). NORTH CAROLINA: Brunswick Co., on Co. Rt. 1335, 2 mi. NW of jct. of Co. Rt. 1340, *Leonard & Radford 2205* (C, CM, E, FLAS, MISS, NO, NY, TENN, TEX, U, UNA, USCH, VDB, WCUH). New Hanover Co., Port Fisher on the Lower Cape Fear Peninsula, *Godfrey 6195* (GH). SOUTH CAROLINA: Bamberg Co., on US 301, 0.3 mi. N of jct. with SC 64, *Bozeman et al. 11400A* (NCU). Georgetown Co., 1,750 ft. due ENE of intersection of US 17 & Belle Isle Gardens Road, *Rayner 1081* (USCH). Hampton Co., 0.2 mi. N of Luray on US Rt. 321, *Ahles & Bell 18288* (FSU, NCU, USF). Marion Co., just E of secondary road 49; 8–10 mi. N of intersection with Great Pee Dee River, *Rayner 1109* (USCH). Orangeburg Co., 2.7 mi. N of Branchville City on (just W of) US 21, *Rayner 1106* (USCH). MEXICO. TABASCO: Huimanguillo, *Cowan 2632* (MO), *2277* (NY), *3111* (MO).

Ludwigia linifolia is a relatively uniform species. Its variability chiefly affects the size of the capsules and the lengths of the bracteoles, which are attached to the sides of the capsule. Its closest affinity is definitely with *L. stricta*, a Cuban endemic, from which *L. linifolia* differs by having narrower leaves, larger floral parts (including sepals, anthers, filaments, and style), and longer fruits and bracteoles. Characters of the two species and the only other petaliferous member of the section, *L. linearis*, are listed for comparison in Table 3.

Ludwigia linifolia has somewhat showy petals and the most prominent nectary disc lobes occurring in sect. *Microcarpium*. The nectary disc is bright yellow and produces copious nectar at anthesis. Herbarium specimens often reveal empty anthers held away from the stigma (mechanical self-pollination has not occurred yet). This observation suggests that *L. linifolia* is probably modally outcrossing, which is corroborated by limited field observations.

Ludwigia linifolia occurs with *L. alata*, *L. curtissii*, *L. glandulosa*, *L. linearis*, *L. microcarpa*, and *L. pilosa* in the field. Natural hybrid populations have, however, been found only between *L. linifolia* ($n = 8$) and *L. curtissii* ($n = 32$). This is contrary to what one would expect for the outcrossing *L. linifolia*. However, experimental hybridizations (Peng, 1988) indicate that artificial hybrids between the diploid *L. linifolia* and plants of any other ploidy level in sect. *Microcarpium* are generally difficult to obtain. Repeated trials with different parental strains were successful in some cases, but the resulting hybrids were usually weak and needed special attention to reach flowering stage. Attempts to synthesize the natural hybrid *L. linifolia* × *L. curtissii* in the experimental greenhouse were unsuccessful.

2. Ludwigia stricta (Wright ex Griseb.) Wright in Wright & Sauvalle, Fl. Cubana 54. 1873. Based on *Isnardia stricta* Wright ex Griseb., Cat. Pl. Cub. 107. 1866. TYPE: eastern Cuba, 1860–1864, *C. Wright 2555* (holotype, GOET; isotypes, G, GH, MO, NY, P, US). Figure 37.

Plants glabrous throughout. Stems erect or ascending from stolons, simple or much branched, 10–60(–85) cm tall. Stolons 5–10 cm long, 1–2.5 mm thick, the leaves elliptic, 7.5–13 mm long, 3–5 mm wide, glabrous, the base attenuate into winged petioles up to 2 mm long. Cauline leaves deciduous from below in late growing season, oblanceolate to narrowly oblanceolate or narrowly elliptic, 11–22 mm long, 2.2–5.5 mm wide, glabrous, the apex acute, the margin with remote, minute hydathodal glands, the base narrowly cuneate into winged petiole 0–1.5 mm long. Stipules minute, ovate or lanceolate, succulent, dark brownish purple, 0.2–0.3 mm long, 0.1–0.2 mm wide. Flowers in upper leaf axils, their subtending leaves

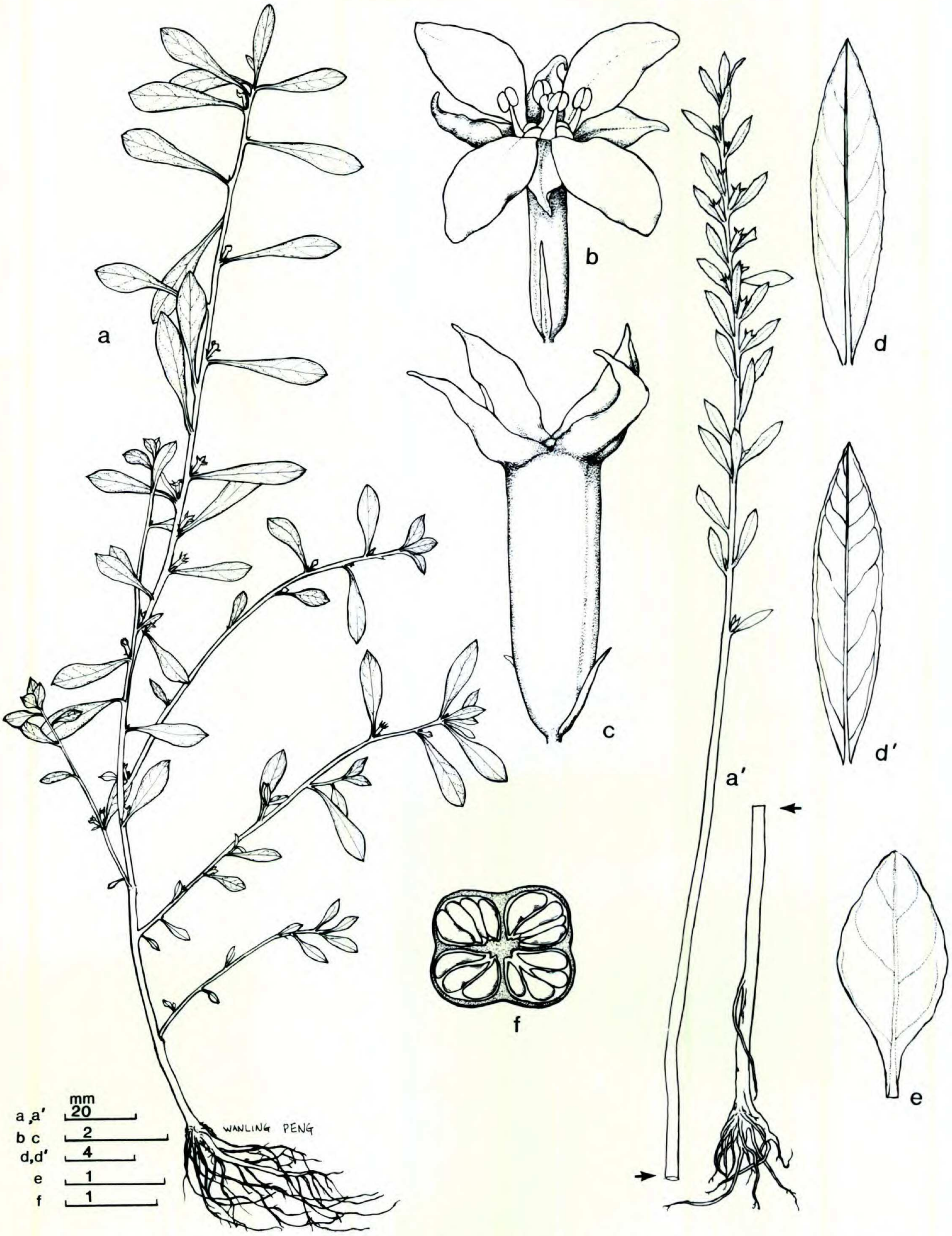

FIGURE 37. *Ludwigia stricta*. a′, c, d, d′, and f from Cuba (*Wright 2555*, US); a, b, and e from plants grown from seeds from Cuba (1982, *Leiva s.n.*, *M 3304*, MO).—a, a′. Habit, stem continues at arrows.—b. Flower.—c. Capsule.—d, d′. Adaxial and abaxial sides of leaf.—e. Petal.—f. Cross section of fruit.

not reduced. Sepals green, narrowly ovate-triangular, ascending, (1.8–)2–3 mm long, 0.9–1.5 mm wide, the apex narrowly acute or acuminate, the margin entire. Petals yellow, elliptic or narrowly obovate, 2.3–2.9 mm long, 1.2–1.3 mm wide, the apex obtuse, the base attenuate. Anthers 0.5–0.7 mm long; filaments 0.75–1.1 mm long. Pollen grains shed as tetrads. Nectary disc yellow, elevated 0.25–0.3 mm on top of the ovary, 1–1.25 mm across, 4-lobed, minutely papillose. Style 0.55–0.9 mm long, glabrous; stigma subglobose, 0.25–0.5 mm across. Capsules cylindrical, 5–6(–7) mm long, 1.6–1.8 mm thick, minutely papillose; pedicels 0–0.9 mm long. Bracteoles attached at capsule base, narrowly lanceolate, 0.7–2.5(–3) mm long, 0.2–0.4(–0.6) mm wide, the margin entire. Seeds reddish brown when mature, elliptic-oblong in outline, slightly curved on both ends, 0.5–0.6 mm long, 0.2–0.25 mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. *Ludwigia stricta* is a uniform species known only from Cuban lagoons and savannas (Fig. 38). Flowering and fruiting from August through November.

Representative specimens examined. CUBA. PIÑAR DEL RÍO: Herradura, *Britton et al. 6613* (NY); Piñar del Río, *Britton et al. 7233* (NY); 3 km S of Herradura, *Ekman 17742* (S). ISLA DE JUVENTUD (ISLA DE PINOS): between Los Indios and La Siguanea, *Ekman 12179* (S); Hotel Colony, *Rostánski 2028* (MO); 1982, *Leiva s.n.* (cultivated, MO).

Ludwigia stricta has a close affinity with *L. linifolia*, which is distributed in the southeastern United States and occurs on the Yucatán Peninsula in Tabasco, Mexico. Both are diploids; they are similar in stature, have four petals, shed their pollen as tight tetrads, have subcylindric capsules that dehisce irregularly from the sides, and have reddish brown seeds with subisodiametric surface cells. A comparison of these two species and the other petaliferous diploid species, *L. linearis*, is presented in Table 3.

Viable seeds of *L. stricta* have become available only recently. Plants have been grown and crossed with all three other diploid species of sect. *Microcarpium* in order to assess their genetic relationships.

3. Ludwigia linearis Walter, Fl. Carol. 89. 1788. *Isnardia linearis* (Walter) DC., Prodr. 3: 60. 1828. TYPE: U.S.A. "the Carolinas": *T. Walter 665* (holotype, BM, Walter Herbarium, p. 66; photograph, MO). Figure 39.

Ludwigia angustifolia Michaux, Fl. Bor.-Am. 1: 88. 1803. LECTOTYPE: U.S.A. South Carolina: near wet ditches, fl. Aug.-Sept., 1785–1796, *A. Michaux s.n.* (P; photographs, GH, MO; isolectotypes, MO, P—2 sheets; lectotype here designated, based on best collection of authentic material at P).

Ludwigia linearis Walter var. *puberula* Engelm. & A. Gray, Boston J. Nat. Hist. 5: 217. 1845. TYPE: U.S.A. Texas: Harris Co., Houston, July 1843, *F. J. Lindheimer 58* (holotype, GH; isotypes, BM, GOET, MO, P, PH, US).

Plants glabrous to densely minutely strigillose or sometimes puberulent, the hairs 0.05–0.15 mm long. Stems erect, often well branched, (22–)50–100(–145) cm tall, often with distinct aerenchyma in lower part. Stolons up to 30 cm long, 0.8–0.25 mm thick, seen in late fruiting season only, the leaves purplish, narrowly elliptic to very narrowly elliptic, 12–23 mm long, 2.8–8.5 mm wide, glabrous to sparingly minutely strigillose, the base attenuate into petioles up to 5 mm long. Cauline leaves green, linear to elliptic linear, 16–60(–85) mm long, 0.9–3.7(–5.6) mm wide, glabrous to densely minutely strigillose or puberulent, the apex very narrowly acute, the margin entire, the hydathodal glands obscure, the base very narrowly acute or cuneate, subsessile. Stipules narrowly ovate or lanceolate, 0.15–0.3 mm long, 0.05–0.15 mm wide. Flowers many, in leaf axils, their flower-subtending leaves not reduced. Sepals green, triangularly ovate to narrowly triangular, the apex acuminate or elongate acuminate to cuspidate, ascending, 2.3–5(–5.6) mm long, 1–3(–3.5) mm wide, glabrous, densely minutely scaly strigillose, strigillose, or puberulent without, glabrous within. Petals yellow, obovate to subrotund, 3–6 mm long, (2–)2.5–5 mm wide, the apex obtuse, the base attenuate. Anthers lanceolate oblong, 1–2 mm long, sporogenous tissue 4–8 packeted; filaments 1.1–2(–2.2) mm long. Packets in the sporogenous tissue opening and shedding tetrad pollen almost simultaneously. Nectary disc yellow, elevated (0.25–)0.35–0.55(–0.7) mm on top of the ovary, 1.3–2.5 mm across, 4-lobed, glabrous to minutely strigillose or strigillose, especially around lobe margins. Style yellowish green, (0.4–)0.7–1.5 mm long, glabrous throughout to densely strigillose, especially in the lower part. Stigma yellowish green, elongated, shallowly 4-lobed on apex, (0.6–)1–1.9 mm long. Capsules elongate obpyramidal, often with a shallow, central, longitudinal groove on each side, 5–10 (–12) mm long, 2–5.5 mm thick, glabrous, densely scaly strigillose, strigillose, or puberulent, subsessile or with distinct pedicels up to 3.5(–5) mm long. Bracteoles subequal, attached near capsule base to 4.5 mm above base or on the pedicel, linear, 0.4–

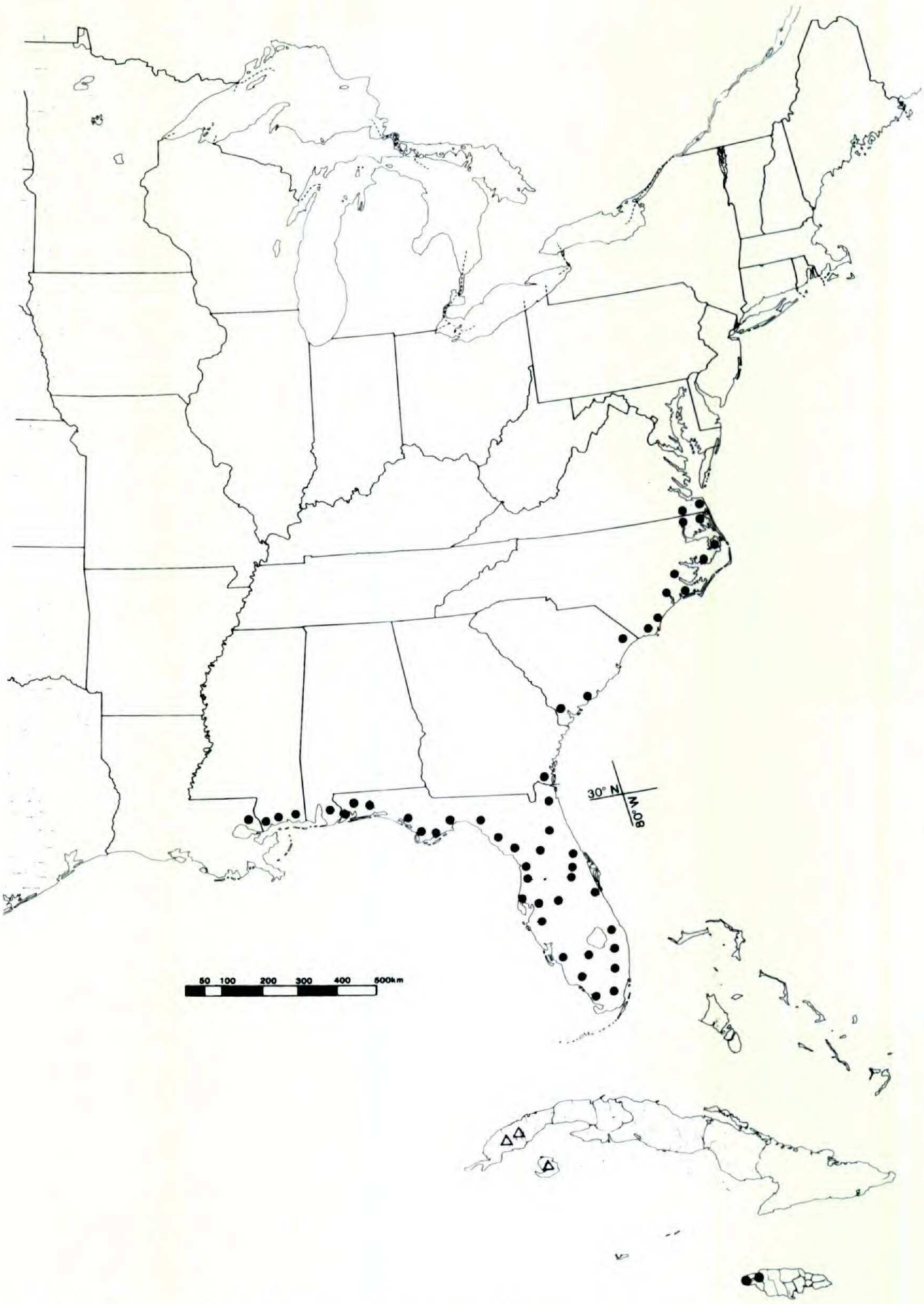

FIGURE 38. Distributions of *Ludwigia alata* (circles) and *L. stricta* (triangles).

4(–7.5) mm long, 0.1–0.3 mm wide, deciduous. Seeds light brown, oblong-elliptic with slightly curved ends, 0.45–0.65 mm long, 0.15–0.25 mm wide, the surface cells oblong, elongate either parallel or transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. *Ludwigia linearis* is common in drainage ditches, along river or stream banks, swales, edges of pocosins, sandy soil in wet meadows, brackish marshes, and occasionally on disturbed ground. It is distributed along the Atlantic coast from southern New Jersey through Delaware, the eastern halves of North and South Carolina, southern Georgia, to its southern limit in central Florida. Westwards, this species extends through the panhandle of Florida and across Alabama, southern Mississippi, and Louisiana, to the central Gulf coast of Texas. To the north, *L. linearis* ranges through eastern Texas and across southern Arkansas, and there is a northward range extension from northern Alabama into Tennessee (Fig. 40).

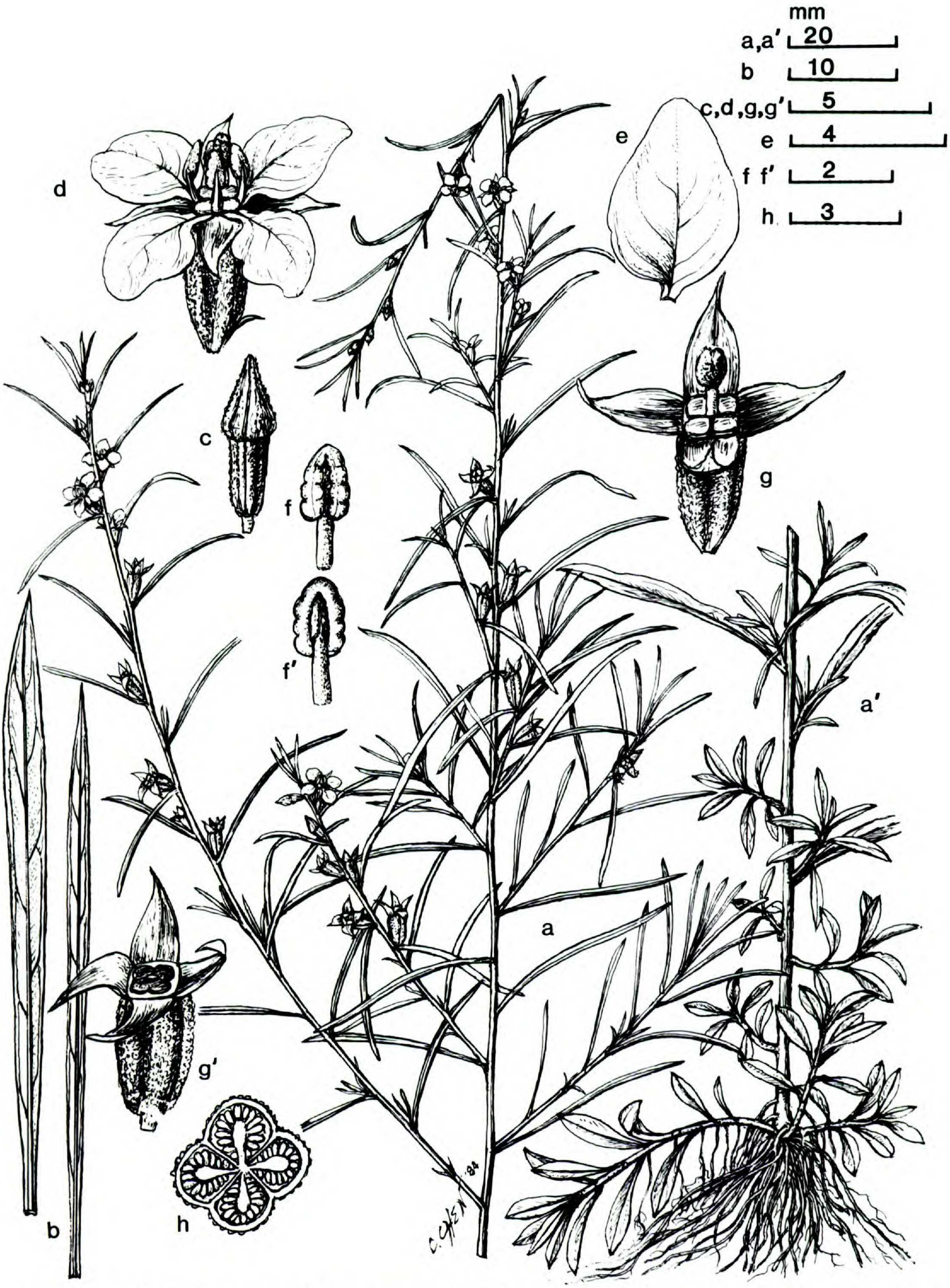

FIGURE 39. *Ludwigia linearis*. All but a′ from South Carolina (Jasper Co., *Boufford et al. 21633*, MO); a′ from Virginia (Nansemond Co., *Fernald et al. 15322*, GH).—a. Habit, erect stem.—a′. Lower stem with basal stolons.—b. Leaves.—c. Flower bud.—d. Flower.—e. Petal.—f, f′. Adaxial and abaxial views of stamen.—g, g′. Immature and mature capsules.—h. Cross section of capsule.

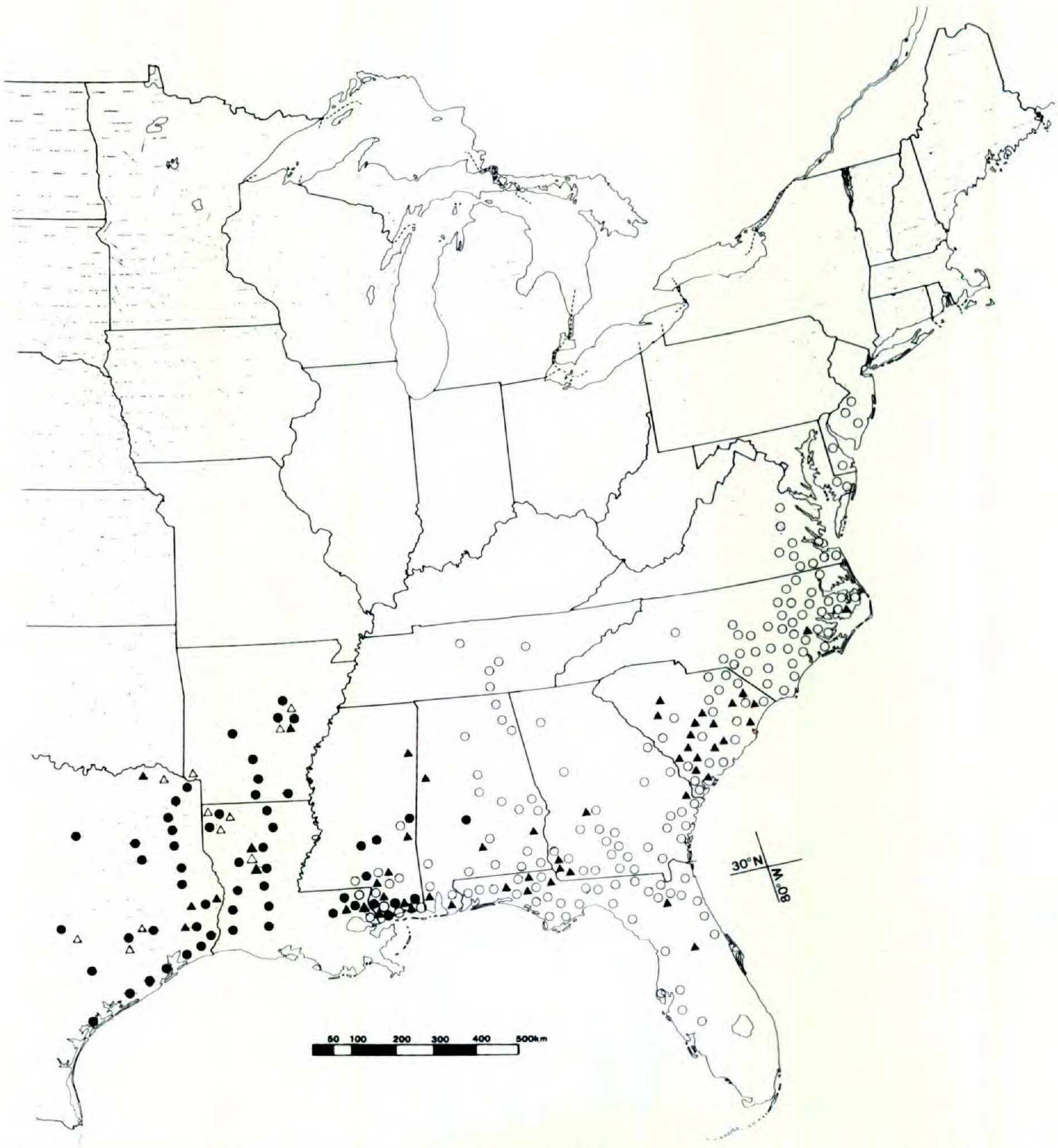

FIGURE 40. Distribution of *Ludwigia linearis*. ○ = subglabrous morph; ● = densely strigillose morph; △ = glabrous morph; ▲ = intermediate morph.

Incorrectly reported from Japan (see discussion). Flowering from late June through September; fruiting from late July through mid December.

Representative specimens examined. (1: subglabrous morph; 2: densely strigillose morph; 3: glabrous morph; 4: intermediate morph—see following discussion.) U.S.A. ALABAMA: Baldwin Co., 1.5 mi. N of Gulf Shores, *Kral 38264* (4, VDB); 13.5 mi. W of Foley on US Hwy. 98, *Raven 18590* (1, DS). Barbour Co., ca. 5 mi. S Eufaula by Lake Eufaula, *Kral 33241* (4, SMU, VDB). Butler Co., ca. 11 mi. N of Georgiana, by US Hwy. 65, *Kral 40891* (1, VDB; mixed with 2). Cherokee Co., by Little River, Canyon Mouth Park, *Kral 43824* (1, VDB). Chilton Co., near Clanton, 1874, *Smith s.n.* (1, UNA). Covington Co., ca. 6 mi. N of Florala on US Hwy. 331, *Davenport 788* (1, UNA). Cullman Co., 1897, *Eggert s.n.* (1, MO). Dale Co., by Choctawhatchee River just N of Newton by AL Hwy. 123, *Kral 54450* (1, VDB). Dallas Co., *Mohr s.n.* (2, F). De Kalb Co., near Mentone, *Ruth 415* (1, NY, US). Elmore Co., 5 mi. N of Wetumpka, by AL Hwy. 9, *Kral 36595* (1, VDB). Escambia Co., 4.6 mi. E of Boykin, just W of Conecuh River by US Hwy. 29, *Kral 44811* (1, VDB). Geneva Co., 3.2 mi. S of Hartford on AL Hwy. 167, *Kral 36723* (1, GA, VDB). Houston Co., E of jct. S of Spring Hill Church, *Clark 7342* (1, NCU). Jackson Co., N of Flat Rock, *Kral 36531* (1, FSU, VDB). Lee Co., near Auburn, 1897, *Earle & Baker s.n.* (1, F, MO, MSC, NY). Macon Co., near Society Hill, 1857, *s.c.* (1, NY). Mobile Co., 2 mi. NE of Theodore on US Hwy. 90, *Kral 29673* (1, FSU, NCU, SMU, VDB); Dauphin Island, near Bienville Blvd., *Deramus D707* (4, NCU, UNA). Pickens Co., S side of Aliceville, *Kral 51383* (4, VDB). Russell Co., 1.3 mi. NW of Phenix City, by US Hwy. 280, *Kral 44243* (1, VDB). Shelby Co., 4 mi. N of jct. AL Hwy 25 & Calera turnoff by US Hwy. 65, *Kral 33584* (1, SMU, VDB). Washington Co., 3.1 mi. S of St. Stevens, *Kral 37216* (1, FLAS, VDB). ARKANSAS: Ashley Co., Lone Pine Prairie, *Demaree 21603* (2, MO, NO, NY SMU, TENN, TEX). Calhoun Co., 10 mi. S of Hampton, *Kral 24536* (2, VDB). Dallas Co., near Fordyce, *Demaree 67870* (1, MO). Garland Co., near Carlisle, *Demaree 38024* (2, SMU). Little River Co., near Ben Lomond, *Demaree 63154* (3, MO). Lonoke Co., near Carlisle, *Demaree*

37980 (2, SMU, VDB; 3, SMU). Prairie Co., near Hazen, *Demaree 37904* (3, SMU, VDB); along Hwy. 70, E of Carlisle, 1956, *Buker s.n.* (4, CM, mixed with 3). Union Co., near El Dorado, *Hoiberg 591* (2, SMU). White Co., 1.2 mi. S of McCrae, by US Hwys. 67, 167, & 64, *Thomas & Smith 15187* (2, DS, SMU, TENN). DELAWARE: Kent Co., near Hamington, 1872, *Canby s.n.* (1, F). Sussex Co., 3 mi. S of Laurel, *Hotchkiss 7919* (1, US). FLORIDA: Alachua Co., E of Gainesville, 1940, *Murrill s.n.* (1, US). Baker Co., near McClenny, *Curtiss 6007* (1, DS, FLAS, GA, GH, MO, NCU, NY, SMU, US). Bay Co., near Lynn Haven, *Godfrey 59120* (1, FSU, SMU). Bradford Co., near Sampson City, *Dennison & Arnold 171* (1, FLAS); W of Lawtey, *Raven 18694* (4, DS). Calhoun Co., 5 mi. W of Blountstown, *Godfrey & Kral 55035* (1, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF). Citrus Co., near Chassahowitzka, *Genelle & Fleming 1562* (1, GA, TENN, USF). Clay Co., near Doctors Inlet, 1939, *Murrill s.n.* (1, DUKE, MO). Columbia Co., near Lake City, 1893, *Rolfs s.n.* (1, F, FLAS, MO). DeSoto Co., near Lacy, 1938, *Arnold s.n.* (1, FLAS). Dixie Co., 4 mi. N of Suwannee, *Godfrey 56179* (1, FSU, GH, NY, USF). Duval Co., ca. 8 mi. from jct. with FL Hwy. 17 on Starrett Rd., *Youree 663* (1, FLAS). Escambia Co., S of Playground Music Center, *Burkhalter 4781* (1, FLAS). Flagler Co., 3 mi. E of Bunnell, 1937, *West et al. s.n.* (1, FLAS). Franklin Co., 41.7 mi. W of jct. US hwys. 98 & 319, *Peng et al. 4351* (1, MO). Gulf Co., between Weewahitchka & Port St. Joe, *Godfrey & Kral 54167* (1, DUKE, FSU, GH, NY). Hamilton Co., 11 mi. E of Suwannee River by FL Hwy. 6, *Godfrey 75386* (1, FSU). Hillsborough Co., 1.5–1.7 mi. S of Hwy. 674, on E side of Taylor Grill Dr., *Peng 4325* (1, MO). Holmes Co., near Westville, *s.c. 4175c* (1, JE; 4, GH, US). Jackson Co., N of Sneads, Lake Seminole, *Godfrey & Houk 61398* (4, TEX); S of Marianna, along Hwy. 71, *Hood 2642* (1, TEX). Jefferson Co., ca. 15 mi. SSW of Monticello, *Kral 5825* (1, FSU, GH, SMU, USF). Lake Co., near Eustis, *Nash 1490* (4, NY). Leon Co., N of Woodville, *Perdue & Godfrey 1858* (1, C, GH, LL, NCU, SMU, TEX, US, USF). Liberty Co., 1 mi. E of Telogia, *Morar 8* (1, DUKE, FSU, MSU). Madison Co., 8 mi. W of Greenville, *Kral 3742* (1, FSU, GH, NCU, SMU). Manatee Co., NE of jct. hwys. 62 & 39, *Shuey 1710* (1, USF). Okaloosa Co., E of Oak Grove by FL Hwy. 2, Yellow River, *Godfrey 75428* (1, FSU). Pinellas Co., Brooker Creek, *Poppleton 698* (1, USF). St. Johns Co., near Crescent Beach, 1941, *West & Arnold s.n.* (1, FLAS). Santa Rosa Co., NW of Maxton, Yellow River, *Godfrey & Houk 62565* (1, FSU). Taylor Co., 18 mi. WSW of Madison, *Kral 3771* (1, FSU, GH, NCU). Union Co., 1 mi. S of Railford, 1940, *Murrill s.n.* (1, FLAS). Volusia Co., S of Seville, 1943, *West & Arnold s.n.* (1, FLAS). Wakulla Co., near St. Marks Refuge, *Morar 17* (1, FSU, NCU, SMU, US, VDB). Walton Co., at Mossy Head, *Godfrey 55244* (1, FLAS, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF); 4 mi. S of Freeport, along Laird Drive, *Davis & Davis 15485* (4, FLAS). Washington Co., 3.5 mi. E of Caryville, *Kral & Godfrey 5960* (1, FSU, USF); S of Chipley along Hwy. 77, *Hood 2836* (4, FLAS). GEORGIA: Bartow Co., ca. 4.5 mi. SE of Adairsville on Cassville Mountain, *Greear 64349* (1, GA, NCU). Berrien Co., ca. 3 mi. W of Alapaha, *Duncan 23488* (1, GA, VDB). Charlton Co., along GA Hwy. 94 between Moniac & St. George, *Jones et al. 23045* (1, GA). Chatham Co., along Dutchtown Road, 1959, *Mellinger s.n.* (1, GH); 4 mi. N of Richmond Hill, *Kral 18947* (4, VDB). Coffee Co., near Douglas, 1900, *Harper s.n.* (1, NY, US). Cook Co., 7.6 mi. SE of Adel, Jim Reeves Pond, *Faircloth 2928* (1, GA, NCU). Decatur Co., 1.5 mi. E of Climax, *Godfrey 75563* (4, FSU). Dooly Co., 0.75 mi. S of Georgia Pacific Plant, S of Vienna by US Hwy. 41, *Godfrey 76005* (4, FSU); 2.7 mi. S-SE of Unadilla, *Harper et al. 16817* (1, GA). Early Co., 2 mi. S of Hilton, *Thorne 6021* (1, US). Echols Co., 2.6 mi. E of Statenville, *Kral 51639* (1, VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on US Hwy. 1, *Peng 4023* (1, MO). Glynn Co., 2 mi. W of Brunswick, *Pyron & McVaugh 279* (GA). Grady Co., 3.5 mi. NW of Calvary, *Faircloth & Faircloth 1509* (1, MO, NCU). Irwin Co., 7.3 mi. SW of Irwinville, at Tift–Irwin Co. line, *Faircloth 5410* (1, GA, NCU). Lanier Co., 1 mi. E of Lakeland, *Faircloth 3605* (1, GA, NCU). Lee Co., 1.5 mi. SW of Smithville, *Pyron & McVaugh 1948* (1, GA). Liberty Co., Camp Stewart near Hinesville, 1943, *Guimm s.n.* (1, CM). Long Co., 4.2 mi. SW of jct. of US hwys. 301 & 25 and GA Hwy. 99, on US hwys. 301 & 25, *Peng 4120* (4, MO); 5.5 mi. W of US Hwy. 301 on GA Hwy. 261, *Bozeman & Radford 1917* (1, NCU). Lowndes Co., 13 mi. E of Valdosta in Grand Bay, *Faircloth 2080* (1, GA, NCU). McIntosh Co., NE section of Sapelo Island, *Duncan 20554* (1, CAS, DUKE, F, GA, GH, MISS, NCU, SMU, TEX, USF). Miller Co., 1.5 mi. W of Colquitt, *Thorne 6716* (1, GH; 4, GA). Pike Co., 0.5 mi. N of Meansville, *Harper 2244* (1, GH, MO, NY). Richmond Co., 1903, *Cuthbert s.n.* (1, FLAS). Screven Co., E of Sylvania, *Eyles 7637* (1, DUKE, GA). Seminole Co., 1.5 mi. E of Donaldsonville, *Godfrey & Clewell 63210* (4, FSU). Thomas Co., near Thomasville, 1903, *Taylor s.n.* (1, TEX). Tift Co., 2.5 mi. W of Alapaha River jct. with Tift & Berrien counties, *Plummer & Pullen 897* (1, GA). Turner Co., 4 mi. WNW of Ashburn on US Hwy. 41, *Ernest 134* (1, NCU). Ware Co., near Waycross, *Eggleston 5078* (1, NY). Wayne Co., near Jesup, *Curtiss 921* (1, CM, F, GA, GH, M, MO, ND, NY, US). LOUISIANA: Acadia Parish, 1.5 mi. W of Midland on US Hwy. 90, *Raven 22095* (2, DS, NCU). Beauregard Parish, 14 mi. W of DeRidder, *Kral 20743* (2, VDB). Bossier Parish, 10 mi. S of Plain Dealing, *Shinners 24488* (3, NO; 4, SMU). Caddo Parish, ca. 2.5 mi. N of Oil City, *Thieret 24467* (3, DS); along LA Hwy. 1, S of jct. LA Hwy. 2, Vivian, *Thomas & Overby 36294* (2, NCU). Calcasieu Parish, ca. 2.5 mi. W of Sulphur, near Stegall, *Thieret 20580* (2, DS, DUKE, FSU, GA, LL, SMU). Evangeline Parish, 6.2 mi. SE of jct. of LA hwys. 106 & 107, *Sullivan 1633* (2, USF). Grant Parish, 4.5 mi. N of Dry Prong, *Shinners 24945* (4, SMU); 1.5 mi. E of US Hwy. 165 opposite LA Hwy. 123, Barrett Quail Farm, *Thomas et al. 2995* (2, NCU, SMU, VDB). Livingston Parish, 5 mi. S of Montpelier, *Thieret 24850* (2, DS). Natchitoches Parish, ca. 4 mi. E of Bellwood, *Kral 16192* (2, VDB). Ouachita Parish, 2 mi. E of Fairbanks, *Thomas et al. 30860* (2, FLAS, GH, SMU, TENN). Rapides Parish, 8 mi. N of Woodworth, *Kral 15828* (2, VDB). St. Tammany Parish, 2.5 mi. N of Talisheek, *Raven 22104* (1, DS, NCU); Hwy. I-59 at Pearl River exit, *Darwin & Sundell 578* (2, NO); 3.7 mi. E of Slidell, along hwy., *Raven 18579* (4, NCU). Tangipahoa Parish, ca. 1.2 mi. E of Arcola, Tangipahoa River, *Thieret 27823* (2, DUKE, FSU, GA); Ponchatoula, *Cocks s.n.* (4, NO). Union Parish, 4 mi. NE of Haile, *Thieret 23691* (2, DS, SMU). Vernon Parish, 2 mi. E of LaCamp, *Kral 15805* (2, VDB). Washington Parish, near Franklinton, *Demaree 46898* (1, DS, SMU, VDB). Webster Parish, ca. 2 mi. W of Springhill, *Allen 8474 &*

Vincent 1798 (3, FLAS, VDB). Winn Parish, 3 mi. N of Winnfield by LA Hwy. 1231-2 at jct. with US Hwy. 165, *Thomas & Cicala 31931* (4, NCU, NY). MARYLAND: Wicomico Co., 6 mi. E of Salisbury, 1872, *Canby s.n.* (1, NY). Worcester Co., near Ocean City, 1909, *Carter s.n.* (1, NY). MISSISSIPPI: Clarke Co., 2.4 mi. NNE of Pachuta, *Jones 10750* (4, MISS). Forrest Co., ca. 3.5 mi. N of Stone Co. line, W of Hwy. 49, *Rogers 4664* (1, MO, NCU); near Ragland Hills, *Rogers 3807* (4, MISS, NCU, VDB). George Co., near Agricola, *Demaree 32789* (1, SMU, VDB). Hancock Co., Kiln Post Office, *Demaree 36311* (1, GH, SMU); Waveland & Hwy. 90, *Jones & Jones 9435* (2, MISS, NCU); on MS Hwy. 43, ca. 5 mi. NE of MS Hwy. 603, *Peng et al. 4363* (4, MO). Harrison Co., near Biloxi, 1900, *Tracy & Lloyd s.n.* (1, F, GH, MSC, US; 4, NY); 2 mi. N of Gulfport, *Jones 10343* (2, GA, MISS). Jackson Co., Ocean Springs, *Seymour 82* (1, CAS, DUKE, F, FSU, GH, MO, MSC, NCU, SMU, TENN, TEX, USF), *Demaree 28232* (2, SMU, TEX, VDB); on MS Hwy. 57, 2.8 mi. N of US Hwy. 90, *Peng et al. 4355* (4, MO). Lamar Co., 5 mi. SW of Hattiesburg, *Ray 5957* (MISS; 1, GA, GH, NCU, NY, USF; 4, NY). Lauderdale Co., S of Lauderdale, *Jones 14990* (1, GA, MISS); E of Chunky, US Hwy. 80 crossing of Chunky River, *Kral 22036* (2, VDB). Marion Co., S of Hwy. 48/35 jct., ca. 3 mi. N of MS–LA border, *Musselman 1238* (2, NCU). Monroe Co., near Amory, 1916, *Bailey s.n.* (4, MISS). Pearl River Co., 5.8 mi. S of Carriere, N of Picayune, *Jones & Hudson 9748* (1, MISS); 1 mi. E of Picayune, *Sargent 9879* (2, MO); 8 mi. NW of Picayune, *Sargent 8376* (4, CAS). Perry Co., 5 mi. E of Runnelstown, *Jones 9587* (1, MISS). Simpson Co., 5.8 mi. S of Puckett and N of Mendenhall, MS Hwy. 13, *Jones 19257* (2, GA, MISS). Smith Co., near Taylorville, *Tracy 8715* (2, F, GH, MO, MSU, NCU, NY, TAES, US). Walthall Co., along MS Hwy. 21, just over LA border, *Kral 19393* (1, VDB). NEW JERSEY: Atlantic Co., near Egg Harbor City, *Mackenzie 5582* (1, DUKE, GH, MO, NY, SMU). Burlington Co., near Atsion, 1879, *Martindale s.n.* (1, F, NY, US). Camden Co., near Atco, 1872, *Commons s.n.* (1, NY). NORTH CAROLINA: Beaufort Co., along NC Hwy. 33, 3 mi. S of jct. of Cox Road, *Duke 54-228* (1, NCU). Bertie Co., 10 mi. E of Windsor, on NC Hwy. 17, *Blomquist 16226* (1, DUKE). Bladen Co., 5.2 mi. W of Dublin, *Duke 5499* (1, NCU). Brunswick Co., 0.2 mi. W of Longwood on NC Hwy. 904, *Peng et al. 3885* (1, MO). Carteret Co., ca. 14 mi. NE of Beaufort on Rt. 70, *Wilbur 9336* (1, DUKE). Chatham Co., 3.1 mi. S of Wilsonville, on Co. Rd. 1008, *Campbell 1077* (1, NCU). Columbus Co., 2.1 mi. NW of Old Dock on NC Hwy. 130, *Leonard & Radford 2192* (1, CM, FLAS, FSU, GA, NCU, NY, SMU, USF, VDB). Craven Co., 0.8 mi. N of US Hwy. 17 on Co. Rd. 1224, *Peng et al. 3737* (1, MO); jct. of US Hwy. 70 & Street Ferry Rd., *Duke 5468* (4, NCU). Cumberland Co., 8 mi. N of Fayetteville, on Hwy. 15A, *Duke 54152* (1, NCU). Dare Co., along US Hwy. 64 N of Manteo, *Duke 54-236* (1, NCU). Duplin Co., 2.5 mi. SSE of Rose Hill on US Hwy. 117, *Ahles 35773* (1, NCU). Edgecombe Co., between Whitakers & Enfield, *Godfrey & Fox 49642* (1, NCSC). Gates Co., 1 mi. NE of Chowan on US Hwy. 158, *Beal 2121* (1, NCSC). Greene Co., 0.7 mi. ESE of Jason, *Radford 40379* (1, NCU). Halifax Co., near Weldon, 1900, *Williamson s.n.* (1, NY). Harnett Co., near Dunn, *Godfrey 6149* (1, DUKE, GH, US). Hoke Co., 4 mi. SSW of Ashley Heights, *Ahles 36379* (1, NCU). Hyde Co., 8.5 mi. SW of Fairfield, *Duke 54-233* (1, NCU); 1.2 mi. NW of Sladesville, *Radford 39039* (4, CTES). Iredell Co., near Statesville, s.d., *Hyanis s.n.* (1, DS). Johnston Co., 4 mi. SE of Benson on NC Hwy. 50, *Lloyd 1121* (1, MO). Jones Co., 0.4 mi. W of Co. Rd. 1105, on Forest Service Rd. 172, *Peng et al. 3798* (1, MO). Lee Co., ca. 1.5 mi. NW of jct. of Deep & Haw rivers, *Beard 745* (1, NCU). Lenoir Co., near Savannah, 2 mi. W of Deep Run, *Radford 31671* (1, NCU). Martin Co., 2 mi. W of Hamilton on NC Hwy. 125, *Duke 54182* (1, NCU). Nash Co., 0.8 mi. S of Taylors Cross Roads and 1.3 mi. E of paved road, *Ahles & Bell 16714* (1, CM, NCU). New Hanover Co., 7 mi. N of Sea Breeze, *Bell 16055* (1, NCU). Northhampton Co., 4 mi. NNE of Jackson, Taylor's Mill Pond, *Beal 2758* (1, NCSC). Onslow Co., 5.5 mi. S of Hwy. 41, on Co. Rd. 1003, S of Comfort, *Peng et al. 3790* (1, MO). Pamlico Co., 4 mi. W of Grantsboro, *Duke 54-225* (1, NCU). Pender Co., 5 mi. NE of Burgaw on NC Hwy. 53, *Radford 5045* (1, GA, NCU). Pitt Co., 3 mi. E of Grimesland, near US Hwy. 264, *Fox 3182* (1, FSU, GH, MO, NCSC). Richmond Co., 3.5 mi. NE of Hoffman at Camp Mackall, *Radford 14440* (1, FLAS, NCU). Robeson Co., 3 mi. N of Lumberton, on NC Hwy. 72, *Duke 54157* (1, NCU). Sampson Co., 1.5 mi. S of Co. Rd. 1003 on US Hwy. 421, *Boufford & Wood 18899* (1, CM, MO). Scotland Co., 4.5 mi. S of Wagram, *Kral 19087* (1, VDB). Tyrell Co., 1.5 mi. NW of Columbia, *Radford 42484* (1, NCU). Washington Co., 4.2 mi. ESE of Skinnersville, *Radford 38893* (1, NCU). Wayne Co., Neuse State Park, *Gillespie CP70* (1, NCSC). Wilson Co., 1.5 mi. WSW of Buckhorn crossroads near NC Hwy. 42, *Radford 44401* (1, WCUH). SOUTH CAROLINA: Aiken Co., near Aiken, 1869, *HWR s.n.* (1, US). Allendale Co., 0.4 mi. E of Barton on Co. Rd. 20, *Ahles & Bell 18420* (4, NCU, U). Bamberg Co., 4 mi. SW of Denmark on Co. Rd. 26, *Ahles 37605* (4, NCU). Beaufort Co., Bluffton, 1873, *Mellichaeux s.n.* (1, NY); 2 mi. SSE of jct. of Co. Rd. 43 & US Hwy. 17 on Co. Rd. 43, *Ahles & Bell 18018* (4, NCU). Berkeley Co., 10 mi. NW of Bonneau, *Godfrey & Tryon 1628* (1, GH, NY); 0.7 mi. E of Interstate 26 and US Hwy. 17-A, *Peng 4390* (4, MO). Calhoun Co., 0.5 mi. NE of jct. of Co. rds. 26 & 27 on 26, *Ahles 35400* (4, NCU). Charleston Co., 4.8 mi. E of SC Hwy. 174 on Hwy. 17, E of Osborn, *Peng et al. 3901* (1, MO); 24.5 mi. N of SC Hwy. 41, on US Hwy. 17, *Peng et al. 3903* (4, MO). Chesterfield Co., Montrose near Hwy. 52, *Radford 15762* (1, TENN). Clarendon Co., 3.5 mi. NE of Turbeville, *Radford 28107* (4, NCU). Colleton Co., 1.2 mi. W of Dorchester Co. line, on SC Hwy. 61, *Raven 20462* (4, DS); 1.2 mi. S of Orangeburg-Colleton Co. line by US Hwy. 21, *Bell 4542* (1, C, NCU). Darlington Co., near Boggy Gully Bay, *Sawyer 2569* (1, USCH). Dillon Co., 1.7 mi. NE of Bingham on SC Hwy. 34, *Ahles 37126* (1, NCU). Dorchester Co., 0.3 mi. S of jct. of hwys. 15 & 178 on 15, *Ahles & Haesloop 37816* (4, NCU). Florence Co., NW of Florence Radio Tower, *Bell 10690* (4, NCU). Georgetown Co., Savannah, *Radford 28679* (4, NCU). Hampton Co., 0.8 mi. NNW of Shirley on Co. Rd. 20, *Ahles & Bell 18255* (1, NCU). Horry Co., Myrtle Beach, *Godfrey & Tryon 1161* (1, DUKE, F, GH, MO, NY, TENN, US); along Waccamaw River at the crossing of SC Hwy. 9, *Raven 18721* (4, DS, NCU). Jasper Co., 0.2 mi. N of Co. Rd. S 27-101 on US Hwy. 17, just S of Ridgeland, *Peng et al. 3935* (1, MO). Lee Co., 3 mi. NE of Woodrow near SC Hwy. 441, *Radford 29422* (1, NCU). Lexington Co., 4.5 mi. W of Edmund, Congaree Creek, *Radford 29890* (1, NCU). Marion Co., ca. 15

mi. S of Britton Neck on Co. Rd. 49, *Bell 11005* (1, NCU); 5 mi. S of Britton's Neck, *Kral 19177* (4, VDB). Marlboro Co., 3.5 mi. E of Wallace, *Radford 19085* (1, NCU). Newberry Co., Billy Dreher Island, *Buff 80* (4, USCH). Orangeburg Co., near Eutawville, *Eggleston 5013* (1, GH, NY); Orangeburg, 1900, *s.c., s.n.* (4, US). Saluda Co., 1 mi. E of Ward, Hwy. 23, *Massey & Massey 3005* (1, NCU); 1 mi. WSW of Ward, *Radford 30358* (4, NCU). Sumter Co., 4 mi. S of Scottsville, near US Hwy. 378, *Radford 29575* (1, NCU). Williamsburg Co., 2.3 mi. NW of Greeleyville, near US Hwy. 521, *Radford 28280* (1, GH, NY, VDB). TENNESSEE: Coffee Co., near Tullahoma, *s.c. 4175* (1, GH, NY, US). Cumberland Co., NE of Crossville, Finger Lake, *Norris & Sharp 16183* (1, TENN). Davidson Co., near Nashville, Cumberland River, s.d., *Gattinger s.n.* (1, DS). Franklin Co., ca. 4.5 mi. SE of jct. of TN hwys. 41A & 4420, Highland Rim Forest Experiment Station, *Wofford et al. 50923* (1, TENN). Warren Co., ca. 1.5 mi. N of Morrison, by TENN Hwy. 55 & power station, *Kral 53781* (1, VDB). TEXAS: Anderson Co., floodplain, *Barkley 13576* (2, F, MO, NY, TEX, US). Angelina Co., 0.5 mi. N of Bouton Lake campgrounds, *Mitchell 4003* (2, LL). Aransas Co., Aransas Wildlife Refuge, *Fleetwood 9344* (2, LL). Bastrop Co., Bastrop, *Tharp 1942* (3, TEX, US). Bowie Co., near Buchanan, 1898, *Eggert s.n.* (2, CM, DS, F, MO, NY). Brazoria Co., near Columbia, *Bush 1542* (2, GH, MO, NCU, NY, US). Brazos Co., 8.5 mi. E of College Station on TX Hwy. 6, *Massey 311* (2, NCU, TEX). Chambers Co., 1932, *Tharp s.n.* (2, TEX). Galveston Co., E side of Hwy. 45, Dickinson, *Waller 3030* (2, GH, TAES). Gregg Co., 1939, *York s.n.* (2, TEX). Hardin Co., near Fletcher, *Palmer 10673* (2, DS, MO); NW of Saratoga, *Kral 21084* (4, VDB). Harris Co., near Sheldon, *Reverchon 3837* (2, MO, NY). Henderson Co., ca. 4 mi. S of Athens, along TX Hwy. 175, *Correll & Correll 33944* (2, LL). Jasper Co., 1.5 mi. N of Kirbyville, *Correll 26762* (2, GH, LL). Jefferson Co., W edge of China, between Rt. 90 & R.R., *Correll 36478* (2, LL). Johnson Co., near Buchanan, 1898, *Eggert s.n.* (2, MO). Lamar Co., E of Manchester on Farm Rd. 195, *Correll & Correll 35909* (4, LL). Lavaca Co., Borcher Ranch, ca. 18 mi. SE of Yokum, *Tharp et al. 49176* (2, TEX). Matagorda Co., ca. 5 mi. SW of Wadsworth, *Sharik S73-1585* (4, MO). Montgomery Co., 17 mi. W of Cleveland, *Kral 21039* (2, VDB); Conroe, 1929, *Tharp s.n.* (3, TEX). Morris Co., ca. 1 mi. W of Naples, *Correll 37471* (2, LL). Nacogdoches Co., *Waller 258* (2, DS, TAES, TEX). Newton Co., along Rt. 87 N of jct. with Rt. 253, *Correll 18719* (2, MO, NY, TEX); 1939, *Tharp s.n.* (4, MO). Orange Co., ca. 1 mi. E of Bridge City, *Correll 34257* (2, LL). Red River Co., N of Clarksville, *Lundell 14011* (3, NY, TEX). Rusk Co., 1879, *s.c., s.n.* (2, F, MO). Travis Co., near Austin, 1929, *Whitehouse s.n.* (2, CAS). Tyler Co., ca. 1.5 mi. S of Warren, E of Rt. 69, *Correll 34015* (4, LL). Upshur Co., 3 mi. S of New Diana, *Shinners 18977* (2, SMU). Waller Co., near Hempstead, *Hall 221* (2, NY; 3, F, mixed with 2, GH, MO, NY, mixed with 2, US, mixed with 2). VIRGINIA: Caroline Co., SE of Guinea, *Fernald & Long 9108* (1, GH). Dinwiddie Co., 12 mi. E of McKenny, *Kral 11336* (1, NCU). Henrico Co., 0.25 mi. W of Elko, *Grimes 4187* (1, GH). Nansemond Co., 3 mi. ENE of Suffolk, *Kral 9508* (1, FSU, NCU). Norfolk Co., 0.5 mi. W of Bowers Hill, *Hubricht B2567* (1, MO). Prince George Co., ca. 3 mi. SE of Petersburg, at head of Poo Run, *Fernald & Long 6652* (1, GH, NY). Princess Anne Co., near Cape Henry, *Fernald & Long 4961* (1, GH, NY, US). Southampton Co., SW of Corinth, Whitefield's Millpond, *Fernald et al. 15320* (1, GH, NY, US). Sussex Co., 3 mi. W of Stony Creek, *Howell 20491* (1, NCU). Warwick Co., near Newport News, 1907, *Long & Long s.n.* (1, US).

The variation pattern of *Ludwigia linearis* is highly complicated as a result of a great deal of intergradation among slightly differentiated geographical races. I have classified the varied populations into four categories: 1) the subglabrous morph, 2) the densely strigillose morph, 3) the completely glabrous morph, and 4) the intermediate morph, which is discussed below.

1. *Subglabrous morph.* Stems sparingly minutely strigillose. Cauline leaves glabrous except for the minutely strigillose margin. Sepals 2.3–4 (–4.5) mm long, 1.3–2.4(–3) mm wide, the apex acuminate, minutely scaly strigillose abaxially. Anthers 1.1–1.6 mm long, the filaments 1.3–1.8 (–2.1) mm long. Nectary disc minutely scaly strigillose around margins of the lobes. Style (0.4–)0.7–0.9(–1.2) mm long, glabrous. Stigma (0.6–)1–1.5 mm long. Capsules densely minutely scaly strigillose, 5–8.5(–10) mm long, 2–4(–5) mm thick, sessile or with a constricted, pedicel-like base. Bracteoles 0.4–1.6(–2.5) mm long. Seed surface cells columnar, elongate parallel to the seed length.

The type of *Ludwigia linearis* Walter belongs to this morph. Plants of this sort are distributed along the Atlantic coast from southern New Jersey through Delaware, eastern Maryland, eastern Virginia, eastern halves of North Carolina and South Carolina, and Georgia, to their southern limit in the central Florida peninsula. They extend westward through the panhandle of Florida and across Alabama and southern Mississippi, reaching eastern Louisiana (Washington and St. Tammany parishes only). Northward, they occur throughout the eastern half of Alabama and extend to central Tennessee.

2. *Densely strigillose morph.* Stems and leaves densely minutely strigillose to puberulent in some cases. Sepals 3–5 mm long, 1.5–2.5(–3.5) mm wide, the apex cuspidate or elongate-acuminate, minutely strigillose or puberulent abaxially. Anthers (1.1–)1.3–2 mm long, the filaments (1.2–)1.5–2(–2.2) mm long. Nectary disc minutely scaly strigillose throughout or only surrounding margins of the lobes. Style (0.6–)0.9–1.5 mm long, glabrous to densely strigillose, especially on the lower part. Stigma (1–)1.3–1.9 mm long. Capsules densely minutely strigillose or puberulent, 5–10 (–12) mm long, 3–5.5 mm thick, the base sessile

or with distinct pedicels up to 5 mm long. Bracteoles 0.5–4(–7.5) mm long. Seed surface cells columnar, elongate transversely to the seed length.

Plants of this morph were recognized at varietal rank, *Ludwigia linearis* var. *puberula*, by Engelmann & Gray (1845). They occur most frequently in central and southern Arkansas, western Louisiana, and the eastern half of Texas. Scattered populations, however, occur east of the Mississippi River in eastern Louisiana and southern Mississippi. A single population was found in Dallas County in southcentral Alabama.

In addition to being much more pubescent than plants of the subglabrous morph, plants of the densely strigillose morph are slightly larger in the size of most floral parts. Furthermore, their seed surface cell pattern is different from that of the subglabrous morph. The cells are elongate parallel to the seed length in the subglabrous morph but are elongate transversely to the seed length in the densely strigillose morph.

3. *Completely glabrous morph.* Characters of this morph are exactly the same as those of the densely strigillose morph, except that the former is glabrous throughout. Indeed, many plants of the completely glabrous morph were collected along with those of the densely strigillose morph. Examples are as follows:

U.S.A. ARKANSAS: Prairie Co., low moist areas in rice paddies, P. O. Hazen, *Demaree 37904* (completely glabrous morph: TEX, VDB-22422, VDB-47595; mixed collection of both the completely glabrous morph and the densely strigillose morph: VDB-33725). Lonoke Co., moist low ground, prairie in rice belt, P. O. Carlisle, *Demaree 22327* (mixed collection of completely glabrous morph and the densely strigillose morph: CAS). LOUISIANA: Bossier Parish, 10 mi. S of Plain Dealing, fire lane in young pine–hardwood stand, sandy loam, *Shinners 24488* (completely glabrous morph: NO; densely strigillose morph: SMU). TEXAS: Waller Co., ditches, Hempstead, *Hall 221* (completely glabrous morph: GH, MO; densely strigillose morph: NY; mixed collection: F, NY—2 sheets, US).

In these cases floral and vegetative characters and even the seed surface pattern are exactly the same in the completely glabrous and the densely strigillose individuals. Plants of these two morphs may well differ only by a single allele that controls the expression of pubescence in plants. It is also worth noting that plants of the completely glabrous morph are only found scattered in Arkansas, Louisiana, and Texas, the main distribution range of the densely strigillose populations. Plants of the completely glabrous morph were previously included by Munz (1944, 1965) as a part of the population of the subglabrous morph (as *Ludwigia linearis* var. *linearis*), which is certainly not appropriate, as discussed above.

Similarly, completely glabrous individuals that are apparently single-allele mutants in populations consisting mainly of densely pubescent plants but are otherwise similar morphologically occur in *Ludwigia hirtella* Raf. (sect. *Ludwigia*; Peng, unpublished).

4. *Intermediate morph.* Any plant that is more pubescent than those of the subglabrous morph and less pubescent than the densely strigillose morph is considered "intermediate" here. The pubescence ranges from scattered minutely strigillose on abaxial midvein and/or submarginal veins to sparingly strigillose on both surfaces of the leaves. The capsule wall is minutely strigillose and not scaly strigillose. Floral characters generally fall in the intermediate range of the subglabrous and the densely strigillose morphs. The seed surface cells, mostly elongate transversely to the seed length, are similar to those of the densely strigillose morph. In some cases, however, the seed surface does not have well-defined cells and is difficult to study. At other times, it is clearly intermediate between that of the subglabrous and the densely strigillose morphs.

Plants of the intermediate morph are widely scattered throughout the range of both the subglabrous morph and the densely strigillose/completely glabrous morphs. They are found in two counties in coastal North Carolina, very well represented in the Coastal Plain of South Carolina, scattered in a few counties in Georgia, Florida, and Alabama, and abundant in Mississippi, where the subglabrous and densely strigillose morphs meet. West of the Mississippi River, they are also found as scattered populations in Arkansas, Louisiana, and Texas, the main distribution range of the densely strigillose morph.

Plants designated as "intermediate morph" here represent an artificial assemblage of plants of *Ludwigia linearis* that may have originated from various combinations of somewhat differentiated populations. For example, the intermediate plants east of the Mississippi River often co-occur with subglabrous plants and may represent hybrids and their derivatives between plants of the subglabrous and of the densely strigillose morphs. On the other hand, intermediate plants that grow west of the Mississippi River may represent hybrids and their derivatives between the completely glabrous morph and the densely strigillose morph, as suggested by the following mixed collections:

U.S.A. ARKANSAS: Prairie Co., along 70, E of Carlisle, *Buker in 1956* (mixed collection of one glabrous plant

TABLE 4. Comparison of subglabrous and densely strigillose populations in *Ludwigia linearis*.

Characters	Subglabrous Populations	Densely Strigillose Populations
Leaves	Completely glabrous on both sides but with minutely strigillose margins	Densely minutely strigillose or puberulent on both surfaces
Bracteole length (mm)	0.4–1.6(–2.5)	0.5–4(–7.5)
Sepal		
Apex	Acuminate	Elongate-acuminate or cuspidate
Length (mm)	2.3–4	3–5(–5.6)
Vestiture	Densely minutely scaly-papillose, the hairs 0.02–0.05 mm long, appressed	Densely minutely strigillose, the hairs 0.06–1 mm long, appressed to ascending
Stigma length (mm)	(0.6–)1–1.5	(1–)1.3–1.9
Style	Glabrous	Glabrous to densely minutely strigillose
Seed surface cells	Elongate parallel to the seed length	Elongate transversely to the seed length
Pedicel length (mm)	0–0.4	0–3.5(–5)

and two intermediate plants). LOUISIANA: Winn Parish, infrequent in open area in dry pine forest ca. 3 mi. NW of Atlanta, in sec. 21 T10N R4W, *Allen 7172* (completely glabrous morph: USF; intermediate morph: NCU).

Plants of the subglabrous populations are somewhat distinguishable from the densely strigillose plants (Table 4) and are separable geographically (the boundary is roughly along the Mississippi River). Engelmann & Gray (1845) formally recognized the distinctiveness of the two morphs. However, with the abundant intergradation between the two races of *L. linearis*, as already noted by Engelmann & Gray (1845), ". . . these characters (of *L. linearis* var. *puberula*) gradually shading away into the ordinary *L. linearis*, . . . ," as well as the occurrence of the completely glabrous populations that have further complicated the character combinations of *L. linearis*, I think a discussion of the variation pattern within this species is more useful than recognizing infraspecific taxa.

Ludwigia linearis was reported as naturalized in marshy areas of Japan (Asai, 1970), and this report was taken up by Osada (1976) in his illustrations of the naturalized plants of Japan. However, an examination of Asai's voucher specimen at TI (Japan: Honshu, Mie Pref., Suzuka-shi, Asahigaoka-machi (Shirako-machi), October 9, 1966, *H. Ohta s.n.*) revealed that it actually represents *L. perennis* L. (sect. *Caryophylloidea*), which is widely distributed in the tropics and subtropics of the Old World and ranges north to Taiwan and southeastern China (Raven, 1963).

Ludwigia linearis can readily be recognized by its sublinear leaves, four yellow petals, and elongate-obpyramidal capsules with a shallow, central, longitudinal groove on each side. The only other species in sect. *Microcarpium* with which *L. linearis* might be confused is *L. linifolia*, which also occurs in the Coastal Plain and the Florida peninsula, but much less commonly. These two species are similar in having very narrow leaves, petaliferous flowers, and elongate capsules. My biosystematic study (Peng, 1988) has shown that they differ by at least a reciprocal translocation. A comparison of morphological characteristics in these two related species and *L. stricta*, which is endemic to Cuba, is petaliferous, and has elongate capsules, is summarized in Table 3.

Ludwigia linearis and the unrelated Latin American congener *L. latifolia* are unique in the genus in having conspicuous, transverse parenchymatous septa in the anthers, which divide the sporogenous tissue into packets (Eyde, 1977; Tobe & Raven, 1986). Before the dehiscence of the anther, however, all of these packets fuse and form one continuous area of sporogenous tissue as a result of disintegration of the septa, leaving the conspicuous vestiges of the distintegrated septa on the inner surface of the anther wall (Tobe & Raven, 1986).

Ludwigia linearis is facultatively outcrossing, having four stamens held away from the stigma at early anthesis and arched over, tightly appressed against the unique, elongate stigma a few hours after anthesis.

Ludwigia linearis is usually very floriferous and has the highest seed set per capsule in sect. *Microcarpium*, about 600 seeds per mature capsule.

Ludwigia linearis co-occurs with *L. glandulosa*, *L. lanceolata*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. sphaerocarpa*, and *L. suffruticosa* in the field. Confirmed natural hybrids include *L. linearis* × *L. glandulosa* (two collections) and *L. linearis* × *L. sphaerocarpa* (one collection). In both cases, hybrids are triploid, fertility as to seed and pollen is nearly zero. Ovaries turn yellowish

or pink after anthesis and then abort. One to four petals are often present in most flowers.

4. Ludwigia glandulosa Walter, Fl. Carol. 88. 1788. TYPE: U.S.A. "the Carolinas": s.d., *T. Walter 612* (holotype, BM, Walter Herbarium, p. 66; photograph, MO).

Plants subglabrous. Stems erect, usually well branched, 10–80(–100) cm tall, glabrous to sparingly minutely strigillose on the ridges formed by the decurrent leaf bases, the hairs ca. 0.05–0.1 mm long. Stolons up to 20 cm long, the leaves purplish, narrowly elliptic, 15–35(–55) mm long, 5–12.5(–20) mm wide, attenuate into petioles 3–10 mm long. Cauline leaves narrowly elliptic to sublinear, sometimes elliptic, those on the main stem 30–120 mm long, 3–25 mm wide, those on the branches usually reduced, 8–45 mm long, 2–10 mm wide; leaves glabrous to sparingly minutely strigillose on abaxial veins, the hairs ca. 0.025–0.05 mm long, apex acute to very narrowly acute, margin entire in outline, densely fringed with microscopic, papillose-strigillose hairs, hydathodal glands often visible, base attenuate, sessile or with petioles up to 15 mm long. Stipules reddish purple, ovate-triangular, succulent, ca. 0.15–0.35 mm long, 0.05–0.25 mm wide. Flowers often numerous, congested in leaf axils. Sepals ovate-deltoid, ascending, 1.1–2.3 mm long, 1–1.75 mm wide, glabrous, apex short acuminate or acute, margin entire, fringed with minute strigillose hairs. Petals 0. Anthers 0.3–0.5 mm long; filaments nearly translucent, 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc greenish, raised ca. 0.25–0.4 mm on top of ovary, 0.6–1.8 mm across, 4-lobed, glabrous. Style pale green, 0.3–0.75 mm long, glabrous. Stigma greenish, subglobose, 0.25–0.5 mm across. Capsules subcylindrical with 4 shallow grooves, each below the midvein of the sepal, 2–7(–9) mm long, 1.3–2(–3) mm thick, glabrous to minutely papillose-strigillose, the hairs 0.02–0.05 mm long, sessile or with pedicels up to 0.35 (–0.5) mm long, well spaced on main stems and primary branches, often congested on short secondary or tertiary branches. Bracteoles flanking capsule base or attached up to 2.1 mm above capsule base, rarely on the short pedicel, lance-linear or linear, 0.35–1 mm long, 0.1–0.35 mm wide. Seeds light brown, kidney-shaped, the ends slightly pointed, ca. 0.5–0.75 mm long, 0.25–0.4 mm thick, surface cells columnar, elongate either parallel or transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

KEY TO THE SUBSPECIES OF *LUDWIGIA GLANDULOSA*

Capsules (4–)5–8(–9) mm long; seed surface cells elongate parallel to seed length ..... a. subsp. *glandulosa*

Capsules 2–4 mm long; seed surface cells elongate transversely to seed length .... b. subsp. *brachycarpa*

The two entities here regarded as subspecies of *Ludwigia glandulosa* were first recognized as distinct by Torrey & Gray (1838–1840). *Ludwigia glandulosa* subsp. *brachycarpa* differs from subsp. *glandulosa* in its smaller stature, narrower leaves, and smaller flowers and capsules. Furthermore, the seed surface pattern of these two entities—a feature that is often diagnostic in *Ludwigia* sect. *Microcarpium*—is sharply distinct, as given in the key.

Ludwigia glandulosa subsp. *glandulosa* is very common and widespread throughout the Atlantic and Gulf coastal plains and the Mississippi Embayment, westward to eastern Texas and southeastern Oklahoma. Subspecies *brachycarpa* ranges just on the western edge of that of the subsp. *glandulosa* in northern Texas and Oklahoma. It grows in the same area as subsp. *glandulosa* throughout much of its range but extends farther south and west. The general distinctiveness of these two subspecies, without doubt, is maintained by their modal autogamy; vegetative reproduction by means of stolons may likewise play a role in preserving favored genotypes.

4a. Ludwigia glandulosa Walter subsp. **glandulosa.** Figure 41.

Jussiaea brachycarpa Lam., Encycl. 3: 331. 1789. TYPE: U.S.A. South Carolina: s.d., *J. Fraser s.n.* (holotype, P, photograph, MO).

Ludwigia heterophylla Poiret in Lam., Encycl. Suppl. 3: 512. 1814. TYPE: U.S.A. "the Carolinas": 1798–1800, *L. A. G. Bosc s.n.* (holotype, P).

Ludwigia cylindrica Elliott, Sketch Bot. S.C. & Ga. 1: 213. 1817. TYPE: U.S.A. South Carolina: Beaufort Co., Burton's Hill, near Beaufort, Aug.–Sept., s.d., *W. Baldwin s.n.* (holotype, CHARL; isotypes, GH, MO, NY; possible isotype, PH).

Stems often reddish, (20–)40–80(–100) cm tall. Cauline leaves elliptic to very narrowly elliptic, those on main stem 32–120 mm long, 4–21 mm wide, those on the branches much smaller, 10–45 mm long, 3–10 mm wide, petioles 1–15 mm long. Sepals ovate-deltoid, the apex acuminate, 1.25–2.3 mm long, 1.15–1.7 mm wide. Petals 0. Anthers 0.3–0.5 mm long; filaments 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc glabrous. Style 0.3–0.5 mm long; stigma 0.35–0.5 mm across. Capsules (4–)5–8(–9) mm long, 1.6–2(–3) mm thick, sessile or with pedicels up to

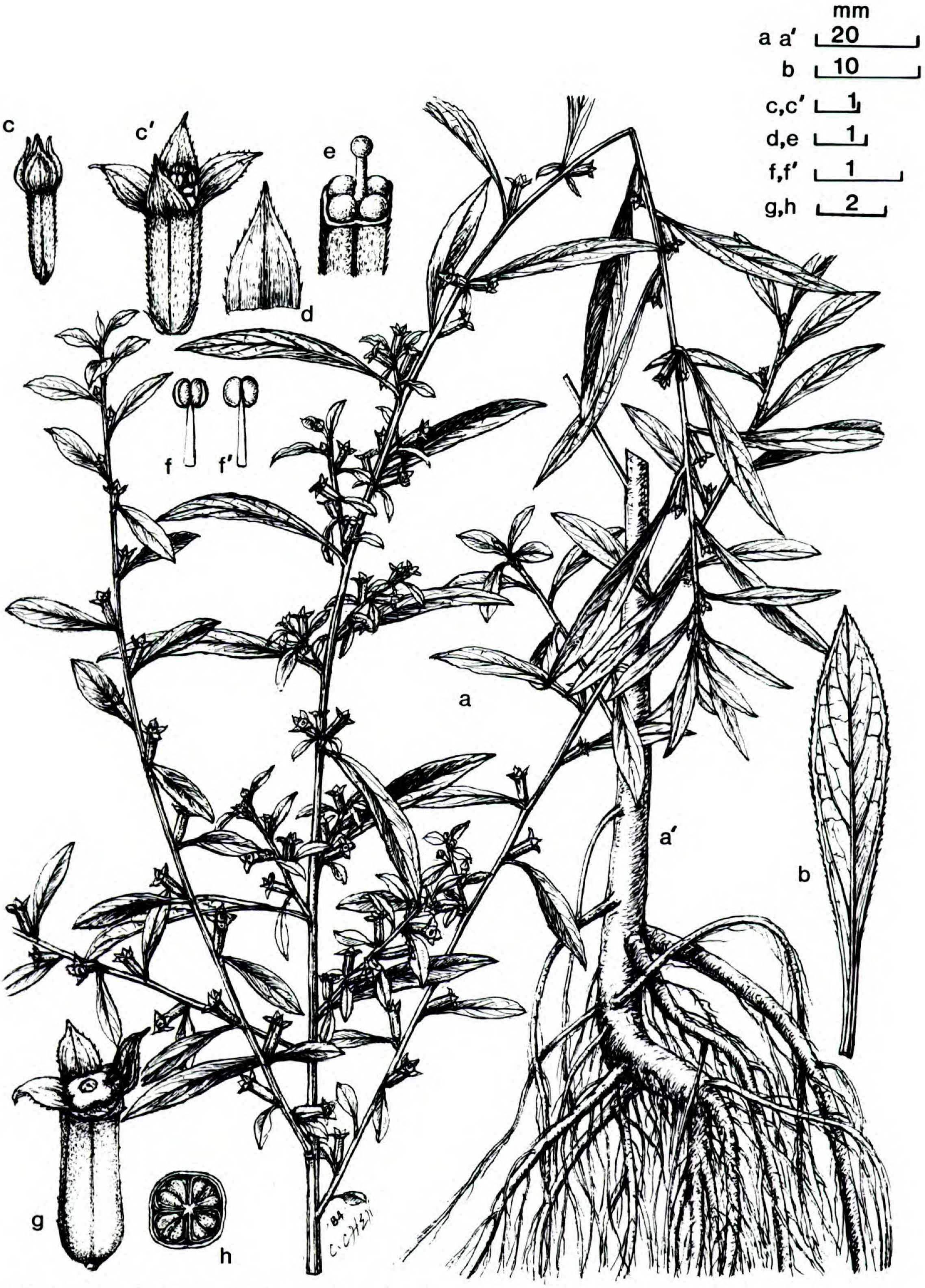

FIGURE 41. *Ludwigia glandulosa* subsp. *glandulosa* (Virginia: Southampton Co., *Fernald & Long 9109*, GH).—a. Habit, upper stem.—a′. Lower stem.—b. Leaf.—c. Flower bud.—c′. Flower.—d. Sepal.—e. Partly dissected flower.—f, f′. Adaxial and abaxial views of stamen.—g. Capsule.—h. Cross section of capsule.

0.35(–0.5) mm long. Bracteoles flanking capsule base or attached up to 2.1 mm above capsule base, rarely on the short pedicel, 0.5–1 mm long, 0.15–0.35 mm wide. Seeds 0.5–0.7 mm long, 0.25–0.35 mm thick, the surface cells oblong, elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. glandulosa* subsp. *glandulosa* are commonly found in roadside ditches, marshes, pond borders, wet meadows, swales, alluvial floodplains, peaty bogs, moist pinelands, swampy woodlands, and occasionally on waste ground. *Ludwigia glandulosa* subsp. *glandulosa* occurs throughout the Coastal Plain from extreme southeastern Virginia southward through eastern North Carolina, South Carolina, south and central Georgia to the panhandle of Florida and westward across southern Alabama, Mississippi, and Louisiana, reaching its western limit in eastern Texas. To the north, this subspecies extends through extreme southeastern Oklahoma, south and central Arkansas, and up the lower Mississippi basin to southeastern Missouri, central and eastern Tennessee, extreme western Kentucky, southernmost Illinois, and southwestern Indiana. Disjunct populations of *L. glandulosa* subsp. *glandulosa* are found in northcentral Missouri (Fig. 43). Flowering from June to September; fruiting from June to October.

Representative specimens examined. U.S.A. ALABAMA: Autauga Co., near Pratville, 1880, *Mohr s.n.* (US). Baldwin Co., 5.2 mi. N of Spanish Fort, by AL Hwy. 225, *Kral 37447* (VDB). Barbour Co., ca. 5 mi. N of Eufaula, on AL Hwy. 165, *Kral 33190* (C, FSU, VDB). Colbert Co., near Littleville, along US Hwy. 43, *Kral 44012* (VDB). Dale Co., near Clayhatchee, *Kral 22078* (VDB). Dallas Co., at mi. 161 of Alabama River, in Miller's Ferry Reservoir, *Wiersema 401* (UNA). Escambia Co., W of Conecuh River by US Hwy. 29, 4.6 mi. E of Boykin, *Kral 44816* (VDB). Geneva Co., NE side of Geneva by Choctawatchee River, *Kral 31911* (FSU, VDB). Greene Co., ca. 1 mi. E of Gainesville, *Harper 4524* (GA, GH, MO, NCU, UNA, WCUH). Houston Co., ca. 6 mi. S of Cottonwood, Spring Creek, *Kral 40043* (VDB). Lee Co., Uchee Creek Pond, 20 mi. S of Auburn on AL Hwy. 37, 1959, *Johnson s.n.* (NCU). Lowndes Co., ca. 1 mi. S of Ft. Deposit, *Kral 40910* (VDB). Macon Co., 19 mi. W of Tuskegee, near US Hwy. 80, *Raven 18562* (DS). Marengo Co., ca. 11 mi. S of Linden along Beaver Creek, *Haynes 6750* (UNA). Mobile Co., *Curtiss 6503* (DS, MO, NY, US). Monroe Co., 3 mi. E of Chrysler on AL Hwy. 59, Shome Creek, *Kral 40948* (VDB). Montgomery Co., 2 mi. N of Montgomery near Tyler-Goodwin Bridge on Alabama River, *Justice & Isely 137* (US). Morgan Co., E of Decatur on AL Hwy. 67, *Kral 36436* (VDB). Perry Co., W of Sprott on Hwy. 183, Cahaba River, *Davenport 779* (UNA). Russell Co., ca. 1 mi. S of Rutherford, *Clark 16208* (NCU). Tuscaloosa Co., 1878, *Vasey s.n.* (F, NY). Wilcox Co., 0.5 mi. E of Camden, 1958, *Williams s.n.* (FSU). ARKANSAS: Ashley Co., near Wilmot, *Demaree 70209* (MO). Calhoun Co., near Thornton, *Demaree 36618* (DS). Clark Co., near Arkadelphia, *Palmer 8069* (CAS, MO, NY). Clay Co., near Corning, *Palmer 6082* (DS, POM, US). Cleveland Co., near Kingsland, *Demaree 23304* (MO, SMU). Columbia Co., near Magnolia, *Demaree 39191* (FSU, GH, NCU, SMU). Conway Co., near Petit Jean Mountain, *Moore 811* (SMU, TENN). Craighead Co., near Lake City, St. Francis River, *Demaree 7076* (F, GH, ND, SMU, TEX, US). Desha Co., near Dumas, *Demaree 48844* (DS, NO, SMU). Drew Co., near Wilmar, *Demaree 66828* (MO). Garland Co., on Big Island in Lake Hamilton, *Demaree 39457* (CAS, SMU, VDB). Grant Co., near Sheridan, *Demaree 19467* (MO, NY, POM, SMU). Greene Co., near Paragould, 1893, *Eggert s.n.* (CM, F, MO, NY, TEX, US). Hempstead Co., near Chidestar, *Demaree 46023* (DS, NCU, SMU). Hot Spring Co., 1896, *Eggert s.n.* (MO). Lee Co., SE of Haynes, S of Clay Hill, *McDaniel 837* (GA). Lonoke Co., near Carlisle, *Demaree 56843* (DS, SMU). Monroe Co., near Holly Grove, *Demaree 37423* (GH, NCU, SMU). Ouachita Co., near Chidester, *Demaree 69674* (MO). Perry Co., near Plainview, *Demaree 46649* (DS, NCU, SMU). Pike Co., near Diamond Mine, *Demaree 51410* (DS). Prairie Co., near Hazen, *Demaree 15457* (DS, MO, NY, SMU). Pulaski Co., near Little Rock, 1885, *Hasse s.n.* (CM, NY). St. Francis Co., 2.5 mi. NE of Madison, upper end of Keithley Lake, *McDaniel 9730* (FSU, MO). Sebastian Co., Massard Prairie, *Armstrong 193* (TEX). Yell Co., near Plainview, *Demaree 46645* (DS, NCU, VDB). FLORIDA: Escambia Co., near Hwy. 4 on Escambia River, *Redfearn & Kral 2777* (FSU, GH). Gadsden Co., River Junction, *Nash 2390* (F, GH, MO, MSC, NCU, ND, NY, US). Gulf Co., near Iola, 1896, *s.c., s.n.* (US). Hamilton Co., ca. 2 mi. S of Genoa, 1946, *Arnold & West s.n.* (US). Holmes Co., 0.5 mi. E of Westville, *Kral & Redfearn 2836* (FSU, GH, NCU). Jackson Co., N of Sneads, Lake Seminole, *Godfrey & Houk 61400* (FSU, SMU, US). Jefferson Co., 3.9 mi. S of Lloyd on FL Hwy. 59, *Raven 18617* (DS). Leon Co., 2 mi. E of Tallahassee, *Godfrey 55604* (FSU, GA, GH, NY, USF). Liberty Co., W side of Ochlockonee River, *Morar 7* (SMU, TEX, VDB). Madison Co., 6.8 mi. W of Greenville on US Hwy. 90, *Raven 18628* (DS). Okaloosa Co., Yellow River by FL Hwy. 2, E of Oak Grove, *Godfrey 75429* (FSU). Santa Rosa Co., 1 mi. E of Milton on US Hwy. 90, *Dille & Dille 412* (MO). Taylor Co., N of Shady Grove, *Godfrey & Kral 54954* (FSU, GH, NY, USF). Wakulla Co., 5 mi. N of Crawfordsville, *Kral 3006* (FSU, GH). Walton Co., at Mossy Head, *Godfrey 55243* (FLAS, GA, GH, NY, SMU, TENN, UNA, USF). GEORGIA: Bibb Co., Ocmulgee River, SE of Macon, 1965, *Welch s.n.* (GA). Bryan Co., on US Hwy. 17, 0.5 mi. SW of GA Hwy. I-95, *Dille & Dille 351* (MO). Camden Co., 2 mi. S of Woodbine, on GA Hwy. I-95, *Dille & Dille 355* (MO). Chatham Co., 12.5 mi. W25°S of Savannah City Hall, *Duncan 21152* (NCU, SMU, US). Decatur Co., Lake Seminole, *Adams 260A* (FSU, NCU, SMU). Dougherty Co., 8 mi. W of Albany, Miller Slough, *Thorne 6758* (GH). Emanuel Co., 0.8 mi. S of Interstate Hwy. 16, on US Hwy. 1, *Peng 4013* (MO). Evans Co., 1 mi. S of jct. of GA Hwy. 169 & US hwys. 25 & 301, on US hwys. 25 & 301, *Peng 4103* (MO). Grady Co., 9.5 mi. SE of Cairo, *Kral 15174* (VDB). Jeff Davis Co., NW of Appling Co. line along Co. Rd., Bullard Creek, *Bozeman 9550* (NCU). Long Co., 4.2 mi. SW of jct. of US hwys. 301 & 25 & GA Hwy. 99, on US hwys. 301 & 25, *Peng*

4119 (MO). Lowndes Co., E side of Nevins Hall, Valdosta State College, *Faircloth 4723* (NCU). McDuffie Co., Bowden's Pond, 11.75 mi. S31°E of Thomson, 1.5 mi. SSE of Arrington Mill, *Duncan 11522* (GA, MO, SMU). McIntosh Co., 3.2 mi. NW of jct. of Cox Rd. & Hwy. 251, on Cox Rd., *Peng 4139* (MO). Screven Co., near Murray Hill, 1907, *Cuthbert s.n.* (FLAS). Seminole Co., paved Co. rd. between Desser & Reynoldsville, *Jones et al. 23645* (GA). Sumter Co., Muckalee Creek, Americus, 1897, *Harper s.n.* (GH, NY). Tattnall Co., Altamaha River, 2 mi. NE of Lane's Bridge, GA Hwy. 169, *Bozeman 5912* (NCU). Thomas Co., Tall Timbers Research, *Godfrey 77177* (FSU). Twiggs Co., Ocumulgee River along GA Hwy. 96, *Bozeman 7539* (NCU). Walton Co., Mossy Head, *Godfrey 55243* (S). Wilkes Co., 7.9 mi. N58°W of Tignal, *Fitzgerald 358* (GA). Worth Co., 5 mi. W of Sylvester, *Thorne 6331* (GA). ILLINOIS: Massac Co., Mermet Lake, SW of Mermet, *Evers 85808* (DS, MO). Pulaski Co., along Cache River, W of Pulaski, *Bailey & Swayne 2710* (NCU). INDIANA: Posey Co., SW corner of Sect. 32 of Point Tp., ca. 10 mi. SW of Mt. Vernon, *Deam 37699* (GH, NY, US). KENTUCKY: Calloway Co., near Backusburg, on W fork of Clarks River, *Athey 2471* (NCU, NY, VDB). Fulton Co., near Hickman, along KY Hwy. 1282, 0.7 mi. E of jct. of KY Hwy. 94, *Athey 2060* (NCU, NY). Graves Co., along KY Hwy. 339, Obion Creek bottoms, *Browne et al. 73E7.8* (NCU, NY). Marshall Co., along KY Hwy. 1523, 0.5 mi. from jct. with US Hwy. 62, *Athey 1132* (NCU, NY). McCracken Co., Pool Road, *Athey 1117* (NCU, NY). LOUISIANA: Acadia Parish, 5 mi. S of Eunice, *Kral 17195* (VDB). Allen Parish, 7.2 mi. W of Kinder, *Shinners 21504* (SMU). Beauregard Parish, 1–1.5 mi. S of Bayou Amacoco, *Ewan 20106* (DS, NO). Bienville Parish, along US Hwy. 20 at Leaterman Creek, W of Gibsland, Sect. 10, T18N, R7E, *Thomas et al. 5209* (SMU, TENN). Bossier Parish, along Clear Lake, S of Eastgate Road, *Balogh 552* (NCU). Calcasieu Parish, 2.5 mi. SW of Starks, *Shinners 25084* (SMU). Caldwell Parish, 3 mi. SW of Grayson, *Shinners 21917* (SMU). Catahoula Parish, 3 mi. W of Harrisonburg, International Paper Co. forest, *Thomas et al. 3979* (DS). DeSoto Parish, 11 mi. W-SW of Mansfield, *Shinners 20349* (SMU). East Feliciana Parish, MacManus RR station, E of Jackson, *Ewan 18772* (NO). Franklin Parish, Winnsboro, Civitan Park, *Thieret 30050* (A, B, FLAS, GA, NCU, SMU, TEX, VDB). Iberia Parish, old air base, New Iberia, *Thieret 31371* (DUKE, FSU, GA, SMU, TEX). Iberville Parish, in woods, 1881, *Langlois s.n.* (NY). Jefferson Parish, 5 mi. S of Marrero, LaFitte Road, *Ewan 17757* (DS, GH, NO, NY). Lafayette Parish, 1 mi. N of Lafayette, *Correll & Correll 9436* (DUKE, GH, NY). Lincoln Parish, 4.5 mi. E of Ruston, *Kral 15736* (VDB). Livingston Parish, Denham Springs, 0.5 mi. N of Range Ave. & US Hwy. 12, *Montz 2253* (NO). Morehouse Parish, ca. 4 mi. NE of Beekman, Sect. 26, T23N, R6E, *Vincent 456* (DUKE, USF). Natchitoches Parish, ca. 1 mi. W of Clarence, along Red River, *Thieret 30247* (DS, DUKE, FLAS). Orleans Parish, near New Orleans, 1836, *Arnott s.n.* (P). Quachita Parish, 3 mi. SW of West Monroe, *Kral 8094* (FSU). Rapides Parish, vicinity of Alexandria, *Ball 640* (F, GH, MO, NY, US). Richland Parish, ca. 1 mi. S of Mangham along LA Hwy. 15, *Vincent 499* (FSU, USF). Sabine Parish, near bridge across Sabine River to TX Hwy. 21, *Demaree 48220* (DS, NO, SMU, VDB). St. Charles Parish, Bonnet Carre Spillway near river road at westguide levee, *Montz 2929* (NO). St. Landry Parish, ca. 4 mi. NW of Grand Coteau, *Thieret 16454* (DS, DUKE, FSU, GA, SMU, VDB). St. Tammany Parish, edge of Pearle River under Interstate Hwy., N of Pearle River, *Raven 18576* (DS, NCU). Tangipahoe Parish, W limits of Hammond, *Raven 22100* (DS). Tensas Parish, ca. 3.5 mi. W of Newellton, along Hwy. to Newlight, *Thieret 23962* (DS, SMU). Terrebonne Parish, near Houma, 1913, *Wurzlow s.n.* (NY). Union Parish, ca. 2.5 mi. S of Lillie off US Hwy. 167, *Vincent 397* (GA). Vermillion Parish, ca. 2 mi. SW of Abbeville, along Vermillion River, *Thieret & Bernard 17863* (DUKE, FSU, SMU, TEX, USF). Vernon Parish, S limits of Leesville on Hwy. 171, *Raven 22088* (DS, NCU). Washington Parish, Mitchell Rd., ca. 3 mi. S of Bogalusa, *Darwin et al. 763* (MO, NO). Webster Parish, 3.5 mi. E of Minden exit on US Hwy. 20, *Kral 27284* (MSU, VDB). West Carroll Parish, 1903, *Moseley s.n.* (US). West Feliciana Parish, 1 mi. NW of Wakefield, *Thieret 24068* (DS). Winn Parish, ca. 2.5 mi. N of Verda, S27, T9N, R3W, *Vincent 166* (DUKE, FLAS, USF). MARYLAND: Somerset Co., Crisfield, 1890, *Holmes s.n.* (MSC, mixed with *L. palustris*). MISSISSIPPI: Adams Co., river floodplain, 9 mi. W-NW of Doloroso, *Jones et al. 13529* (FSU, MISS, NCU). Amite Co., roadside of Longleaf Plantation, ca. 5 mi. S of Liberty, *Jones et al. 19946* (GA, MISS). Bolivar Co., 3.5 mi. W of Duncan on MS Hwy. 444, *Pullen 70420* (MISS). Calhoun Co., 6.9 mi. E of Bruce on MS Hwy. 32, *Pullen 70696* (MISS). Chickasaw Co., 4.7 mi. E of Vardaman on MS Hwy. 8, *Temple 3535* (GA, MISS, NCU). Clarke Co., 3 mi. S of Pachuta, *Ray 5072* (GA, GH, NCU, NY, TENN, USF). Clay Co., Tibbee Creek bottoms, ca. 3.8 mi. S of West Point on US Hwy. 45W, *Pullen 69839* (MISS). Coahoma Co., near Lyon, 1927, *Rhoades s.n.* (F, NY). De Soto Co., open R/W of US Hwy. 55 & adjacent Coldwater River bottoms, ca. 1 mi. N of Tate-De Soto Co. line, *Pullen 70877* (MISS). Forrest Co., Ragland Hills, Leaf River, *Rogers 3810* (MISS, VDB). Franklin Co., edge of Clear Springs Rec. Area, *Jones 10089* (MISS). George Co., banks of Cedar Creek, Agricola P.O., *Demaree 35758* (GH, SMU). Greene Co., along Leaf River on MS Hwy. 98, *Jones & Hudson 8486* (MISS). Hancock Co., along Jordan River S of Kiln, *Jones & Jones 14145* (MISS, TEX). Harrison Co., near Biloxi, *Tracy 6463* (GH, MO, MSU, NCU, NY, US, VINDOB). Holmes Co., ca. 2.5 mi. S of Tchula near open R/W of MS Hwy. 12, *Pullen 70402* (MISS). Humphreys Co., on MS Hwy. 12, 2.6 mi. NW of Holmes–Humphreys county line, *Pullen 69973* (MISS). Jackson Co., Pascagoula airport rd., *Jones & Jones 14941* (GH, MISS, NCU). Jasper Co., 6 mi. via rd. from Enterprise along Souinbuey Creek, *Jones 15162* (MISS, TEX). Jefferson Co., 6 mi. N-NW of Church Hill at base of loess bluffs, *Jones & Noble 10171* (MISS). Jones Co., 6.6 mi. NE of Moselle on MS Hwy. 11, *Raven 18569* (DS, NCU). Kemper Co., power line R/W, 2.9 mi. W of Scooba, Hwy. 16, *Jones 18867* (MISS, TENN). Lauderdale Co., RR tracks S of Lauderdale, *Jones 14995* (GA, MISS, SMU, USF). Leake Co., under power line, ca. 1 mi. N of Pearl River, S of Wiggins on Hwy. 13, *Jones et al. 18127* (MISS). Lincoln Co., 11 mi. W of Brookhaven, *Webster & Wilbur 3296* (GH, NY, SMU, US). Madison Co., 14 mi. SE of Canton at Ross Barnett Reservoir, *Jones 19454* (MISS). Monroe Co., ca. 3.5 mi. W of Amory, vicinity of Tombigbee River bridge on US Hwy. 278, *Pullen 671032* (MISS). Montgomery Co., 5.1 mi. E of Duck Hill on MS Hwy. 404, *Pullen 701013* (MISS). Neshoba Co., 5.1 mi. NW of Choctaw Indian Reservation, W of Philadelphia on MS

Hwy. 16, *Temple 11996* (MISS). Panola Co., 2.4 mi. W of Tallahatchie River bridge on MS Hwy. 6, *Temple 5893* (GA). Pearl River Co., 2 mi. W of Picayune, *Sargent 10226* (CAS, MO). Pike Co., 5 mi. SW of McComb, Percy Quin State Park, *Jones & Jones 19523* (MISS, VDB). Prentiss Co., 3.7 mi. E of Baldwyn on S side of MS Hwy. 366, *Temple 6212* (GA, MISS). Quitman Co., 3.5 mi. N of Tallahatchie–Quitman county line on MS Hwy. 3, *Pullen 641453* (GA, MISS). Rankin Co., ca. 3 mi. SE of Johns on MS Hwy. 18, *Temple 11960* (GA, MISS). Scott Co., edge of lake, Raworth Recreation Area, between Morton and Forest, *Jones et al. 17874* (FLAS, MISS). Sharkey Co., ca. 7 mi. W of Holly Bluff in Delta National Forest, *Pullen 691196* (MISS). Simpson Co., 2 mi. N of D'Lo on MS Hwy. 49, *Jones 14065* (MISS, VDB). Smith Co., 5.1 mi. S of Pulaski and N of Trenton on MS Hwy. 481 at stream, *Jones 19151* (MISS, SMU). Tishomingo Co., MS Hwy. 72 at Yellow Creek, *Coleman 48529* (TENN). Union Co., 5.7 mi. SE of Etta on county rd., around creek bridge, *Pullen 70842* (MISS). Washington Co., 1 mi. E of Longwood, *Pullen 65302* (MISS, NCU). Wilkinson Co., 8.4 mi. SW of MS Hwy. 33 near Crosby on MS Hwy. 563, *Temple 12148* (MISS). Winston Co., Nanih Waiya St. Pk., S-SE of Louisville, *Jones et al. 18231* (MISS, VDB). Yazoo Co., 3.5 mi. NW of jct. US Hwy. 49E on MS Hwy. 3, *Temple 10189* (GA, MISS). MISSOURI: Butler Co., swamps in Blue Spring, 1892, *Eggert s.n.* (MO). Cape Giradeau Co., 3 mi. W of Arbor on Hwy. 25, *Steyermark 64138* (F). Dunklin Co., near Campbell, 1893, *Bush s.n.* (GH, MO, ND, NY). Pemiscot Co., 7 mi. S of Portageville, *Steyermark 9131* (MO). Stoddard Co., woods bordering Swan Pond, T28N, R10E, Sect. 35, 4 mi. S of Advance, *Steyermark 66146* (MO). Sullivan Co., near Paw Paw, *Bush 152* (MO). Wayne Co., 3 mi. SE of Chaonia, T26N, R7E, Sect. 32 & part of 33, *Steyermark 6197* (F, MO). NORTH CAROLINA: Anson Co., Brown's Creek on NC Hwy. 74, W of Wadesboro, *Duke 54-111* (NCU). Beaufort Co., under bridge 300 yds. N of Wynns Service Station on US Hwy. 17, *Duke 54-176* (NCU). Bertie Co., under bridge of Conine Creek on US Hwy. 70 E of Williamston, *Duke 54-261* (NCU). Bladen Co., 2.9 mi. N of Clarkton on road to Bluefield, *Ahles & Leisner 33338* (NCU). Brunswick Co., 4 mi. S of jct. with Hwy. 17 on NC Hwy. 133, *McCrary & Ahles 1227* (NCU). Camden Co., ditch at Belgrade, *Duke 54-247* (NCU). Chatham Co., 7 mi. E of Pittsboro, RR R/W at US Hwy. 64 crossing, *Campbell 1046* (NCU). Chowan Co., 0.6 mi. W of Perquimans–Chowan county line on US Hwy. 17, *Ahles & Duke 47864* (NCU). Columbus Co., 2.3 mi. N of Tabor City on NC Hwy. 410, *Duke 54-91* (NCU). Craven Co., 0.8 mi. N of Hwy. 17 on Co. Rd. 1224 (rd. to Tuscarora), *Peng 3739* (MO). Cumberland Co., 1 mi. N of Beard, the 0.4 mi. W-NW, *Ahles & Leisner 33545* (NCU). Durham Co., jct. of Co. Rd. 1242 (Biscayne Rd.) and NC Hwy. 54, along New Hope Creek, *Boufford & Wood 18861* (MO). Edgecombe Co., beside Swift Creek on Hwy. 85, *Duke 54-71* (NCU). Gates Co., 1 mi. NE of Chowan River on NC Hwy. 158, *Beal 2132* (NCSC). Greene Co., 4 mi. W of Farmville on US Hwy. 70, *Duke 54-168* (NCU). Harnett Co., Byrd's Mill Pond, S of Bunn Level on NC Hwy. 15a, *Duke 54-149* (NCU). Hertford Co., 1.1 mi. NE of Como then 1.9 mi. E-NE on dirt rd., *Ahles & Duke 45982* (NCU). Hyde Co., 0.5 mi. N of Scranton Creek, on US Hwy. 264, *Duke 54-280* (NCU). Johnston Co., Neuse River, 3 mi. N-NE of Cox Mill, *Radford 27789* (NCU). Jones Co., 0.4 mi. W of Co. Rd. 1105 (Catfish Rd.) on Forest Service Rd. 172 (Murey Branch Rd.), E-SE of Maysville off NC Hwy. 58, *Peng et al. 3801* (MO). Lee Co., 2 mi. NW of Sanford along Big Buffalo Creek, *Houck 359* (NCU). Martin Co., 2.3 mi. SW of Robersonville, *Radford 39396* (NCU). Nash Co., near Moccasin Creek and US Hwy. 264 W of Middlesex, *Radford 44350* (NCU, US). Northampton Co., 1 mi. W of Margarettsville, then 0.3 mi. S, *Ahles & Haesloop 52529* (NCU). Pamlico Co., 5 mi. W of Grantsboro on NC Hwy. 55, *Duke 54-227* (NCU). Pasquotank Co., 1.5 mi. N of Nixonton by Halls Creek, *Ahles & Duke 51239* (NCU). Pender Co., 4 mi. W of Montague on Black River, *Radford et al. 7388* (NCU). Perquimans Co., 2 mi. E-NE of Chowan–Perquimans county line, *Ahles & Duke 48002* (NCU). Pitt Co., 2 mi. E of Pactolus near NC Hwy. 33, *Radford 39717* (TEX). Robeson Co., 4.7 mi. S of Fairmont on NC Hwy. 41, *Duke 54-143* (NCU). Rowan Co., 0.1 mi. N of Stanly–Rowan county line, *Ahles & Haesloop 57224* (NCU). Stanly Co., 3 mi. E of Richfield on NC Hwy. 49, *Duke 54-103* (NCU). Union Co., 3.5 mi. E of New Salem, *Ahles 34111* (NCU). Wake Co., 6.5 mi. S of Raleigh Yates Pond, *Beal 1837* (NCSC). Washington Co., 3.2 mi. NW of Creswell, *Radford 38902* (NCU). Wilson Co., 4.6 mi. W of Wilson, *Radford 40791* (NCU). OKLAHOMA: Atoka Co., 3.5 mi. SW of Atoka, *Cory 56815* (SMU). Choctaw Co., near Hugo, *Palmer 8348* (CAS, MO, NY, US). LeFlore Co., near Page at pond margin, *Stevens 2626* (DS, GH, MO, NY, US). Marshall Co., 2.5 mi. SE of Enos, Happy Hollow, near Lake Texoma, *Goodman 6696* (RSA, TEX). McCurtain Co., 3 mi. S and 1 mi. E of Eagletown, *Taxodium* swamp, *Waterfall 10406* (SMU). Sequoyah Co., 0.5 mi. SE of Blackgum on OK Hwy. 100, *Wallis 5565* (SMU). SOUTH CAROLINA: Aiken Co., North Augusta, near Savannah River, *Ahles & Crutchfield 55638* (NCU). Allendale Co., Coosawhatchie River, 3.4 mi. SE of Fairfax on County Hwy. 21, *Bell 5064* (NCU, USCH). Bamberg Co., Salkehatchie River on US Hwy. 321-301, NE side of river, *Ahles & Haesloop 30547* (NCU). Beaufort Co., 1.9 mi. W of Co. Hwy. 111 on Co. Hwy. 33, *Bell 3759* (NCU, U). Berkeley Co., Santee River, 3 mi. NE of Pineville, *Godfrey & Tryon 644* (CAS, DUKE, F, GH, MO, NY, TENN, US). Charleston Co., 24.5 mi. N of SC Hwy. 17, vicinity of Buck Hill Recreation Area, S of McClellenville, *Peng et al. 3896* (MO). Cherokee Co., 0.7 mi. S of US Hwy. 29A on dirt road along Broad River, *Ahles & Haesloop 31925* (NCU). Chesterfield Co., 1 mi. W of McBee in the Sandhills, *Godfrey 8025* (F, GH, MO, NY, TENN, US). Clarendon Co., NE shore of Lake Marion, ca. 4.5 mi. SW of St. Paul, off US Hwy. 15, *Bradley & Sears 3561* (MEXU, MISS). Colleton Co., 1.2 mi. W of Dorchester county line on SC Hwy. 61, *Raven 20461* (DS). Darlington Co., damp flats, *Smith 2001* (NCU). Dillon Co., Sweat Swamp, ca. 3 mi. N of Little Rock on Co. Hwy. 192, *Ahles & Leisner 32234* (NCU). Dorchester Co., 0.4 mi. N of Reevesville on Co. Hwy. 16, *Ahles & Leisner 31905* (NCU). Georgetown Co., 2.8 mi. NE of Yauhannah, Pee Dee River near US Hwy. 701, *Radford 28609* (NCU). Greenwood Co., 1.5 mi. N of Ninety Six, Wilson Creek near SC Hwy. 246, *Radford 26581* (NCU). Hampton Co., 0.8 mi. N-NW of Shirley on Co. Hwy. 20, *Ahles & Bell 18249* (NCU). Horry Co., along Waccamaw River at crossing of SC Hwy. 9, *Raven 18724* (DS, NCU). Jasper Co., roadside ditch at S end of Ridgeland, *Raven 18715* (DS, NCU). Kershaw Co., 8 mi. NW of Camden on Wateree River, *Radford 27668* (NCU). Marlboro Co., 9 mi. SW of Bennettsville, Pee Dee River, near US Hwy.

52, *Radford 15477* (CM, FLAS, NCU, SMU). McCormick Co., 6 mi. SE of Clarks Hill, Savannah River near SC Hwy. 28, *Radford 30647* (NCU, VDB). Orangeburg Co., 3.9 mi. S-SE of Eutawville on Co. Hwy. 104 along Sandy Run, *Ahles 35003* (NCU). Richland Co., 15 mi. below Columbia along Congaree River, 1965, *Batson s.n.* (USCH). Saluda Co., near US Hwy. 178 at Mayson, *Radford 26906* (NCU). Sumter Co., 4 mi. E-NE of Shiloh, Jordon Swamp, *Radford 27500* (FSU, NCU). TENNESSEE: Carroll Co., edge of cat-tail pool, *Svenson 4385* (GH). Crockett Co., Cypress Creek N of Bells, *Sharp & Clebsch 6754* (TENN). Franklin Co., near Huntland, *Svenson 10403* (GH). Grundy Co., N of Mt. View, *Godfrey 69774* (FSU, NCU). Hardeman Co., N of Middleburg, *Sharp & Clebsch 8208* (TENN). Henderson Co., Beech River SW of Chesterfield, *Sharp et al. 9289* (TENN). Lake Co., Reelfoot Lake, 1924, *Jennings & Jennings s.n.* (CM). Montgomery Co., 1.5 mi. NW Sadlersville by US Hwy. 41, *Kral 48384* (VDB). Obion Co., near Bayoudechien, Walnut Log, *Sharp & Clebsch 6207* (TENN). Shelby Co., McKellar Lake, Ensley Engineer yard, *Rogers 34826* (TENN). White Co., 9 mi. N of Sparta, swamp S of Cookeville, *Norris & Sharp 16241* (TENN). TEXAS: Angelina Co., near Redland, *Lewis & Oliver 5245* (DH). Bastrop Co., near Bastrop, *Tharp 224* (GH, NY, TEX). Bowie Co., near Texarkana, 1894, *Letterman s.n.* (F, MO, NY, TEX, US). Brazoria Co., Cockleburr Slough above bridge on Shell Rd., San Bernard Refuge, *Fleetwood 10159* (SMU). Brazos Co., Fish Lake behind Easterwood Airport, College Station, *Massey 309* (NCU, TAES, TEX). Cass Co., ca. 2.5 mi. SW of McLeod along Frazier Creek, *Correll 30113* (TEX). Fayette Co., near Muldoon, *Ripple 51-914* (TEX). Galveston Co., S edge of Alta Loma, *Correll & Correll 38997* (LL). Gonzales Co., *Bogusch 943* (TEX). Gregg Co., ponds along Sabine River S of Longview on TX Hwy. 149, *Correll & Correll 31856* (TEX). Grimes Co., Navasota Bottoms, 1927, *Parks & Cory s.n.* (TAES). Hardin Co., 16.5 mi. NW of Saratoga, *Kral 21046* (DH, DS, VDB). Harris Co., near Crosby, 1921, *Fisher s.n.* (DH, US). Henderson Co., 9.5 mi. S of Athens, *Shinners 19124* (SMU). Jackson Co., 8 mi. E of Edna, Navidad River floodplain, *Webster & Wilbur 3142* (SMU, US). Jasper Co., near Harrisburg, 1875, *Joor s.n.* (F). Lamar Co., ca. 5 mi. NE of Paris on TX Hwy. 195, *Correll 37518* (TEX). Liberty Co., 5.7 mi. E of Liberty, *Raven 19425* (DH, FLAS, NCU). Limestone Co., 4 mi. SE of Donie on Hwy. 80 & 0.5 mi. E on Hwy. 39, *Lipscomb 3088* (SMU). Marion Co., 9.6 mi. NW of Jefferson, *Shinners 30257* (SMU). Montgomery Co., 4.5 mi. E of Montgomery, 1950, *Henry s.n.* (CM). Nacogdoches Co., *Waller 254* (DH, TAES, TEX). Newton Co., E side of Bon Wier, *Kral 20731* (VDB). Orange Co., along Sabine River near bridge, E of Orange, *Correll 26792* (TEX). Panola Co., 8 mi. NE of Carthage, Sabine River, *Shinners 15656* (SMU, TAES). Polk Co., McCordell Lake, E of TX Hwy. 59, *Nixon et al. 5363* (NCU). Rains Co., 9.2 mi. S of Point, *Van Vleet 678* (SMU). Red River Co., ca. 7.5 mi. N of Clarksville along TX Hwy. 37, *Correll 37495* (NY, TEX). Titus Co., N of Winfield, *McGregor 750* (SMU). Upshur Co., 5 mi. N of Ore City, along Cypress Creek, *Correll 13171* (NY, SMU, TEX). Waller Co., near Hempstead, 1872, *Hall s.n.* (F, GH, NY, US). Wood Co., 4 mi. W of Mineola, *Kral 1239* (FSU). VIRGINIA: Greensville Co., SW of Haleys Bridge, Fontaine Creek, *Fernald et al. 6653* (GH). Nansemond Co., ca. 7 mi. E-NE of Suffolk, *Kral 13765* (FSU, VDB). Norfolk Co., S of North Landing, *Fernald & Long 4076* (GH, NY). Prince George Co., near Gary Church, *Fernald & Long 6307* (GH, NY). Princess Anne Co., near Rosemont, *Fernald & Long 4962* (GH, US). Southampton Co., near bridge over Three Creek, N of Drewryville, 1970, *Churchill s.n.* (MSU). Warwick Co., near Newport News, 1907, *Long & Bartram s.n.* (NY). York Co., E of Tabb's, *Fernald & Long 8787* (GH).

Ludwigia glandulosa is distinctive in being the only tetraploid species in sect. *Microcarpium* with cylindric capsules. The other three species with elongate capsules are the diploid, petaliferous, narrow-leaved *L. linearis*, *L. linifolia*, and *L. stricta*. Raven & Tai (1979) suggested that *L. linearis* is similar to *L. glandulosa* and might be directly related to it. The biosystematic study of Peng (1988), however, demonstrated that the genetic relationship between the diploid *L. linearis* and the tetraploid *L. glandulosa* is not any closer than that between *L. linearis* and other tetraploids. Furthermore, it has been shown that no extant diploids are involved directly in the formation of any tetraploid species in sect. *Microcarpium*.

Ludwigia glandulosa subsp. *glandulosa* is known to occur together with subsp. *brachycarpa*, *L. linearis*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. sphaerocarpa*, and *L. palustris* (sect. *Dantia*) in the field. It has been known to form natural hybrids with all but *L. microcarpa*, an extreme selfer, and the facultatively outcrossing *L. linifolia*. Attempts to synthesize *L. glandulosa* × *L. linifolia* in the experimental greenhouse also failed (Peng, 1988), presumably owing to incompatible genomes. Artificial hybrids between *L. glandulosa* subsp. *glandulosa* and *L. microcarpa*, however, were healthy and floriferous.

Duke (1955) was the first to record a natural hybrid population of *Ludwigia glandulosa* subsp. *glandulosa* × *L. pilosa*, although he did not fully describe the situation he observed. Tetraploid hybrids like this and others are usually fertile and are intermediate in such diagnostic characters as vestiture, sepal and bracteole length, capsule shape and size, seed surface pattern, and whether pollen is shed singly or as tetrads. Triploid natural hybrids involving *L. glandulosa* subsp. *glandulosa* and diploids like *L. linearis* and *L. palustris* may be floriferous but are highly sterile as to pollen and seeds. Their ovaries turn yellowish or pink and dehisce early. *Ludwigia glandulosa* subsp. *glandulosa* (stems erect, leaves alternate) × *L. palustris* (stems prostrate, leaves opposite) generally resembles *L. glandulosa* subsp. *glandulosa* but has slightly broader leaves and smaller flowers. The stems are erect and then prostrate and erect again in some cases; the leaves are alternate like *L.*

glandulosa subsp. *glandulosa*. By contrast, hybrids of *L. glandulosa* subsp. *glandulosa* and *L. linearis* are similar to *L. linearis*, having some yellow petals and narrow leaves. The number of petals on each flower varies from 0 to 4.

4b. Ludwigia glandulosa Walter subsp. **brachycarpa** (Torrey & A. Gray) Peng, Ann. Missouri Bot. Gard. 73: 490. 1986. Based on *L. cylindrica* Elliott β *brachycarpa* Torrey & A. Gray, Fl. N. Am. 1: 524. 1840, non *Jussiaea brachycarpa* Lam., Encycl. 3: 331. 1789. *L. glandulosa* Walter var. *torreyi* Munz, Bull. Torrey Bot. Club 71: 164. 1944, illeg. subst. LECTOTYPE: U.S.A. Texas: Austin Co., San Felipe, "third collection," 1833–1834, *T. Drummond 84* (GH; isolectotypes, GOET, K—2 sheets, W; Peng, Ann. Missouri Bot. Gard. 73: 490. 1986). Figure 42.

Stems sometimes reddish, 10–55(–90) cm tall. Cauline leaves linear-elliptic to linear, sometimes very narrowly elliptic, those on main stem 30–50(–70) mm long, 3–5(–10) mm wide, those on the branches 8–36 mm long, 2–3(–8) mm wide, sessile or with petioles up to 10 mm long. Sepals ovate-deltoid, the apex acute or short acuminate, 1.1–1.9 mm long, 1–1.75 mm wide. Petals 0. Anthers 0.3–0.5 mm long; filaments 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc obscurely minutely papillose. Style 0.35–0.75 mm long; stigma 0.2–0.35 mm across. Capsules 2–4 mm long, 1.3–2 mm thick, sessile or with pedicels up to 0.15 mm long. Bracteoles flanking capsule base, 0.35–0.75 mm long, 0.1–0.2 mm wide. Seeds 0.55–0.75 mm long, 0.3–0.4 mm thick, the surface cells oblong, elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia glandulosa* subsp. *brachycarpa* are usually found along ditches, in low meadows, coastal prairies, seeps in sandy woods, moist sinkholes in granites, and old clay fields. This subspecies occurs along the Gulf coast, from extreme southwestern Louisiana to Nueces County, Texas, and northward through eastern Texas to southcentral Oklahoma (Fig. 43). Flowering and fruiting from April to November.

Representative specimens examined. U.S.A. LOUISIANA: Calcasieu Parish, 1 mi. S of Holmwood, *Ewan 21343* (NO). Cameron Parish, 2 mi. W of jct. of State hwys. 82 & 27, *Peng et al. 4367* (MO). OKLAHOMA: Atoka Co., 6 mi. SE of Lane on OK Hwy. 3, *Massey & Massey 2496* (MO, NCU, SMU). Carter Co., N of Ardmore, *Goodman 5961* (GH, RSA, SMU). Coal Co., 5 mi. SE of Centrahoma on OK Hwy. 3, *Massey 2484* (NCU, SMU). Love Co., 5 mi. SE of Ardmore in Lake Murray State Park, *Crutchfield 3449* (LL). TEXAS: Aransas Co., near Lenoir's Landing, Copano Bay, *Correll & Correll 18905* (GH, LL). Bastrop Co., *Tharpe 870* (TEX). Brazoria Co., Columbia, 1980, *Bush s.n.* (MO, NY). Brazos Co., Fish Lake behind Easterwood Airport, *Massey & Reaux 586* (LL, NCU). Burnet Co., 2 mi. N of Marble Falls, Granite Mt., 1946, *Barkley & Copeland s.n.* (NY). Calhoun Co., Port O'Connor, 1930, *Tharpe s.n.* (TEX). Dallas Co., Dallas, 1877, *Reverchon s.n.* (NY). Denton Co., Lake Dallas Fish Hatchery, *McCart 1894* (NY, TEX). DeWitt Co., western part of county, 1941, *Reidel s.n.* (TEX). Fort Bend Co., 9.1 mi. N of Rosenberg on road to Fulshear, *Raven 19398* (DS, RSA, TEX). Galveston Co., 1942, *Nelson s.n.* (GH, MO, TEX). Gonzales Co., 7 mi. S of Gonzales, *Correll & Johnston 17481* (LL). Harris Co., 200 mi. S of TX Hwy. 59 near jct. with Santa Fe RR, 200 mi. N of Overhead Door Co., *Tranverse 1490* (F, SMU, TEX). Jasper Co., Harrisburg, 1875, *Joor s.n.* (LSU, US). Jefferson Co., on Hwy. 90, 12 mi. W of Beaumont, *Munz & Gregory 23458* (RSA). Lavaca Co., ca. 18 mi. SE of Yoakum, *Tharpe, Rogers & York 49177* (TEX). Limestone Co., ca. 5.5 mi. SE of Donie on 80 across Hwy. 39, *Lipscomb 2908* (SMU). Matagorda Co., near College Port, 1929, *Tharpe s.n.* (TEX). McLennan Co., MKT RR at Gapland crossing, *Smith 863* (TEX). Montague Co., 2 mi. NW of Stoneburg, *Shinners 26622* (SMU). Nueces Co., Mustang Island, ca. 3 mi. S of Port Aransas, *Jones 1837* (SMU). Red River Co., 1.5 mi. S-SW of Bogata, *Shinners 20405* (SMU). Refugio Co., Austwell, 1929, *Tharpe s.n.* (TEX). San Patricio Co., 3 mi. NE of Ingleside, *Jones 932* (SMU). Travis Co., Austin, *Tharpe 870* (TEX, US). Waller Co., Hempstead, *Hall 219* (F, NY, US).

Plants of *Ludwigia glandulosa* subsp. *brachycarpa* occur in the western range of the species and are frequently found in the same county as the typical subspecies, but mixed collections suggesting that they occur side by side are known only in the following: TEXAS: Fort Bend Co., 1 mi. NW of Arcola, water-filled roadside ditch of swampy brushlands, *Raven 19405* (DS, mixed collection of two plants of subsp. *glandulosa* and one plant of subsp. *brachycarpa*; FLAS, subsp. *brachycarpa* only).

Natural hybrid populations between these two subspecies are known in two cases from OKLAHOMA: Atoka Co., ca. 0.25 mi. S of small community of Boehler and SE of Atoka, *Taylor 20332* (VDB), and TEXAS: Galveston Co., ca. 2300 block of Broadway, San Leon, *Waller 3822* (GH). These hybrids are intermediate in stature, leaf shape and size, and (more diagnostically) in fruit size (4–5 mm long) and seed surface (which exhibits a mixture of columnar cells that are elongate, transversely elongate, and sometimes oblique to the seed length).

5. Ludwigia polycarpa Short & Peter, Transylv. J. Med. Assoc. Sci. 8: 581. 1835. *Is-*

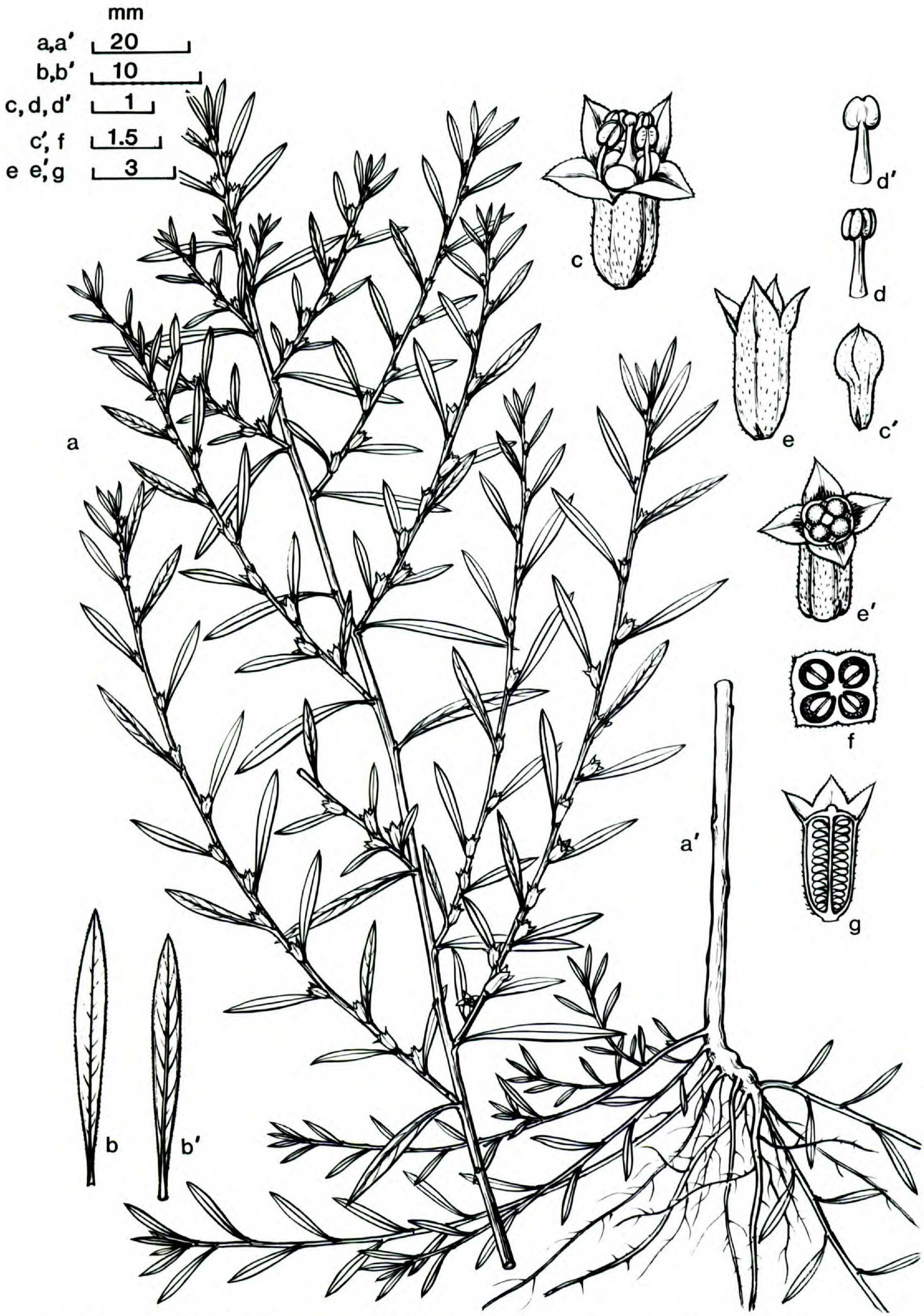

FIGURE 42. *Ludwigia glandulosa* subsp. *brachycarpa* (Louisiana: Cameron Co., *Peng 4367*, MO).—a. Habit, upper portion of erect stem.—a′. Lower stem with stolons.—b, b′. Adaxial and abaxial views of lower leaf.—c. Flower.—c′. Flower bud.—d, d′. Adaxial and abaxial views of stamens.—e. e′. Mature capsule.—f. Cross section of capsule.—g. Longitudinal section of capsule.

FIGURE 43. Distribution of *Ludwigia glandulosa* subsp. *glandulosa* (circles) and *L. glandulosa* subsp. *brachycarpa* (triangles).

nardia polycarpa (Short & Peter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. LECTOTYPE: U.S.A. Kentucky: marshes around Louisville, s.d., *H. A. Griswold s.n.* (PH; isolectotypes, DWC, GH, NY, 2 sheets; lectotype here designated). Figure 44.

Plants glabrous. Stems erect, well branched, (10–)25–60(–85) cm tall, the leaf base decurrent and forming ridges 0.15–0.25 mm broad, these sometimes minutely strigillose; aerenchyma well developed on lower stems when submersed. Stolons short, several from the erect stem base, 2.5–15 (–22) cm long, 1–2.3 mm diam., usually seen only in late flowering season, frequently branching from the nodes; internodes short, leaves often clustered on stolon apex and overlapping, narrowly elliptic or oblanceolate, 7.8–20(–32) mm long, 2.4–8 (–12) mm wide, glabrous, the margin entire or remotely denticulate, papillose-serrulate; petioles 0–5 mm long. Cauline leaves very narrowly oblong-elliptic, 35–110 mm long, 4–10(–17) mm wide, the apex narrowly acute or acuminate, the margin entire, densely minutely papillose-serrulate except for the lowest ⅕, this usually smooth, hydathodal glands obscure, the base very narrowly cuneate or long attenuate into winged petiole 1–10 mm long. Stipules dark purplish, narrowly to broadly ovate, succulent, 0.15–0.35 mm long, 0.1–0.25 mm wide. Flowers many, sessile or nearly so in leaf axils, sometimes borne almost to the base of stems; flower-subtending leaves not reduced. Sepals greenish, triangularly ovate, the apex elongate acuminate, spreading horizontally with reflexed tips, 2.5–4.5 mm long, 1.5–3.2 mm wide, glabrous, the margin entire, minutely papillose-serrulate. Petals 0. Anthers 0.5–0.85 mm long; filaments yellowish green, 0.7–1.5 mm long, the base dilated. Pollen grains

FIGURE 44. *Ludwigia polycarpa* (Massachusetts: Franklin Co., 1949, *Delevoryas s.n.*, DS).—a. Habit, upper portion of stem.—a′. Stem base with newly formed stolons.—b. Leaf.—c. Portion of narrowly ridged branch.—d. Portion of branch with mature capsules.—e. Flower bud.—f. Flower.—f′. Partly dissected flower to show stigma, style, and nectary disc.—g, g′. Adaxial and abaxial views of stamens.—h. Sepal.—i. Bracteole.—j. Capsule.—k. Cross section of capsule.

shed as tetrads. Nectary disc yellowish green, raised 0.5–0.75 mm on ovary top, 1.8–3 mm across, 4-lobed, glabrous. Style yellowish green, 0.5–0.8 mm long, glabrous; stigma greenish yellow, cuboid, 0.4–0.8 mm long, distinctly 4-lobed on the apex. Capsules oblong-obovoid with constricted base, obscurely 4-sided with rounded corners, 4–7 mm long, 2.5–5 mm thick, glabrous to obscurely minutely strigillose; pedicels 0.1–0.3 mm long. Bracteoles flanking the capsules, attached 0.5–2.5(–3) mm from capsule base, linear-lanceolate with a swollen base, 3.5–6.5(–8) mm long, 0.4–1(–1.3) mm wide, the margin minutely papillose-serrulate. Seeds light brown, narrowly oblong with curved ends, 0.5–0.6 mm long, 0.2–0.3 mm wide, the surface cells elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia polycarpa* grow in ditches; on moist prairie; on alluvial ground of ponds, lakes, and rivers; in marshes; in swales; along edges of lagoons; and in low fallow fields. Contrary to all other species in sect. *Microcarpium*, *L. polycarpa* is centered primarily in the central Midwest, ranging from southcentral Missouri, eastern Kansas, eastern and northeastern Nebraska, northward and eastward across Iowa and southern Minnesota into central Wisconsin and the Upper Peninsula of Michigan. In the east, this species occurs in extreme southern Ontario and the eastern part of the Lower Peninsula of Michigan. *Ludwigia polycarpa* extends southward through western and southern Ohio, northcentral Kentucky, and western West Virginia. Scattered populations occur in central Virginia, southcentral Pennsylvania, Massachusetts, and Connecticut. A highly disjunct, presumably introduced population has been recorded from Kootenai County, Idaho (Fig. 45). Flowering from June to September; fruiting from July to October.

Representative specimens examined. U.S.A. CONNECTICUT: Hartford Co., *Bissell & Clark 245* (B, C, CAS, CM, DS, F, GA, GH, M, MO, NO, NY, S, TENN, TEX, US, USF, W). IOWA: Appanoose Co., 1896, *Fitzpatrick s.n.* (MO). Black Hawk Co., old creek bed, *Burk 847* (MO). Clinton Co., NW ¼ Sect. 6, Grant twp., *Cooperrider 2899* (NCU). Decatur Co., marshes, 1899, *Fitzpatrick s.n.* (F, MSU, NY). Emmet Co., wet ground, 1884, *Cratty s.n.* (DS). Fayette Co., borders of ponds, 1893, *Fink s.n.* (GH). Johnson Co., N of Homestead, 1924, *Shimek s.n.* (NY). Lee Co., ca. 1.25 mi. W-SW of Ft. Madison, *Davidson et al. 684* (TEX). Louisa Co., *Davidson 4035* (TEX). Palo Alto Co., 5 mi. E of Ruthven in a pond S of the viaduct over Hwy. 18, *Hayden 9416* (GH, MO, NY, US). Polk Co., *Van Bruggen 3152* (NY, SMU). Poweshiek Co., rich slough beside US Hwy. 6, about 1.5 mi. W of Victor, *Russell 815258* (USF). Story Co., Ames, 1877, *Arthur s.n.* (P). Warren Co., 1 mi. NW of Indianola, *Van Bruggen 3105* (?). Washington Co., 3 mi. S of Crawfordsville, *Wagenknecht 874* (F). Webster Co., Fort Dodge, 1904, *Somes s.n.* (NY). IDAHO: Kootenai Co., head of Fernan Lake, Coeur d'Alene, *Rust 1353* (NY, US). ILLINOIS: Adams Co., 1842, *Holtman s.n.* (CM). Champaign Co., near Urbana, *Jones 12683* (NY, SMU). Cook Co., Elk Grove Forest Preserve, *Kral 9384* (FSU, NCU, VDB). DuPage Co., W of Lacey road near the Milton–Lisle Township line NE of Lisle, *Swink 1828* (F). Gallatin Co., 1 mi. N of Shawneetown, *Evers 85336* (MO). Hancock Co., Augusta, 1847, *Mead s.n.* (F, MO). Henderson Co., Mississippi bottoms near Oquawka, s.d., *Patterson s.n.* (F, MO, US). Iroquois Co., 1888, *Moffatt s.n.* (NY). Lake Co., 5 mi. SW of Waukegan, *Kral 3324* (FSU). Massac Co., Mermet Lake, SW of Mermet, *Evers 85807* (DS). Menard Co., Athens, 1861, *Hall s.n.* (F, NY, GH). Ogle Co., Oregon, 1888, *Waite s.n.* (NY). Piatt Co., 1881, *Seymour s.n.* (USF). Pike Co., NW of Pleasant Hill, *Evers 93796* (NCU). St. Clair Co., vicinity of Kingshighway, *Neill 15378* (NCU, MO). Sangamon Co., Auburn, 1882, *Bigler s.n.* (GH). Stark Co., Wady Petra, *Chase 197* (F, GH, MSU). Will Co., 2 mi. SE of Custer Park, *Steyermark 64838* (F). Winnebago Co., 1858, *Bebb s.n.* (GH, UPS). INDIANA: Blackford Co., 2 mi. W of Mollie on S side of road, *Deam 325* (MO, US). Delaware Co., along NYC RR, ca. 3 mi. W of Yorktown, *Friesner 18365* (SMU, TEX, W). Fayette Co., *Gardner 545* (NY). Howard Co., 4 mi. NW of Kokomo, *EK 22* (US). Jackson Co., about 0.75 mi. S of Chestnut Ridge, *Deam 14039* (NY, S). Lake Co., Whiting, 1893, *Britton s.n.* (NY). Martin Co., old river slough just N of White River and W of road 45, *Tryon 4161* (DUKE). Newton Co., about 5.5 mi. SW of Lake Village, *Deam 56715* (CM, GH). Porter Co., Dune Park, *Lansing 1539* (F). Posey Co., in Scuffle pond, ca. 8 mi. SW of Mt. Vernon, *Kriebel 8378* (ND). Pulaski Co., ditch on Jasper-Pulaski game reserve, 1 mi. W Rd. 43, 1.5 mi. S Rd. 10, *Friesner 16176* (CAS, FLAS, NY). Randolph Co., Clarke, 1897, *Unbach s.n.* (US). Warrick Co., 6 mi. W of Boonville on the bank of Big Pigeon Creek, *Deam 24336* (GH). Wells Co., 1897, *Deam s.n.* (F). KANSAS: Douglas Co., 4 mi. SE Lawrence, *McGregor 15001* (US, NCU, SMU). Jackson Co., marshes, *Clothier 1141* (GH, MO, NY, US). Linn Co., 1 mi. S Boicourt, *Stephens 44334* (NCU). Miami Co., 1883, *Oyster s.n.* (CAS). KENTUCKY: Boone Co., pond about 1,000 ft. inland from Aurora ferry (just opposite Aurora, Indiana) along Hwy. ca. 2 mi. W of Petersburg, along Ohio River, *Thieret 50135* (VDB). Fayette Co., Lexington, *Short s.n.* (NY, GH). MAINE: Franklin Co., E side Pine Hill, Deerfield, *Ahles 64607* (DS, NCU, SMU). Hampshire Co., Hockanum Rd., Northampton, *Ahles 86398* (GA, SP). Middlesex Co., Winter pond, Winchester, *Raven 16514* (MO). MICHIGAN: Genesee Co., Linden Park, 1903, *Farwell s.n.* (DS). Houghton Co., near Houghton, 1916, *Dodge s.n.* (LL). Macomb Co., wet thicket W edge of woods, frequent, *Loughridge 4390* (GH, B). Monroe Co., along Detroit to Toledo RR between Stein and S Otter rds., 1972, *Churchill & Thompson s.n.* (MSU). Oakland Co., Hubbard marsh, 1916, *Chandler s.n.* (MSU, US). St. Clair Co., near Port Huron, 1893, *Dodge s.n.* (SMU, TEX, TENN, S). Tuscola Co., Akron Tp., 1895, *Davis s.n.* (S). Van Buren Co., Marsh Keeler, *Pepoon 619* (MSU). Washtenaw Co., 3 mi. W of Third Sister Lake, *Hermann 8357* (DS, F, MO, NY, US). Wayne Co., ca. 4 mi. out from Detroit, 1851, *Cooley s.n.* (MSU). MINNESOTA: Chisago Co., *Wis-*

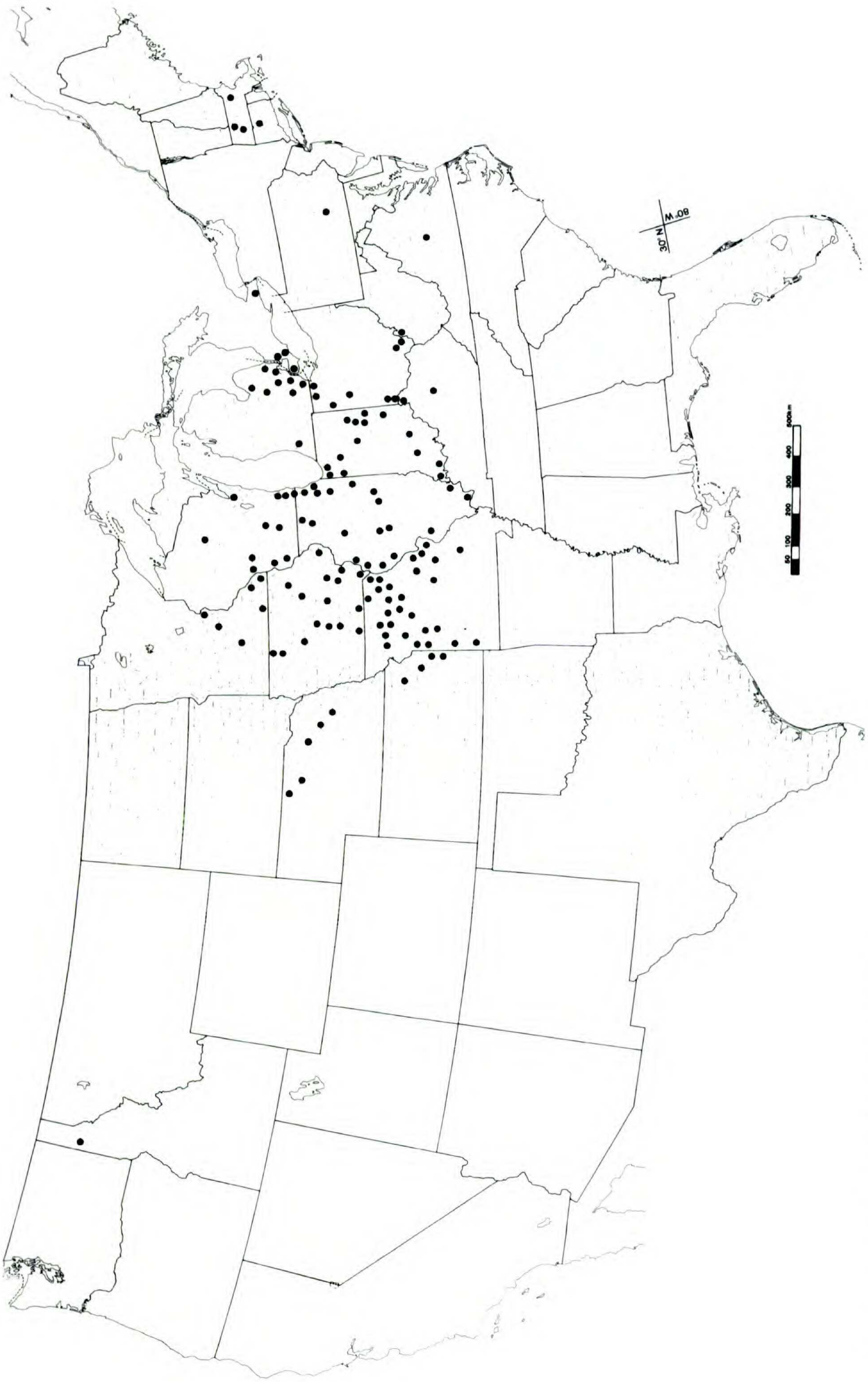

FIGURE 45. Distribution of *Ludwigia polycarpa*.

lizenus 503 (MO). Hennepin Co., near Minneapolis, 1892, *Burglehaus s.n.* (MO, MSU). Houston Co., along backwater of the Mississippi River, 2 mi. S of La Crescent, *Moore 26506* (CAS, EH, NCU). Mower Co., near Taopi, *Rosendahl et al. 7261* (GH). Nicollet Co., edge of the Red Rock outcrops 3–4 mi. W of Courtland, 1947, *Moore & Huff s.n.* (GH, US). Winona Co., river bank, 1897, *Holzinger s.n.* (NY). MISSOURI: Cass Co., in valley of Grand River, 3.5–4 mi. NW of Archie, *Steyermark 66785* (F, UPS). Chariton Co., Little Chariton River, 4 mi. NE of Keytesville, *Steyermark 26456* (MO). Clark Co., 1892, *Bush s.n.* (MO). Daviess Co., Old Grand River, S of Packwood Lake, 4.5 mi. W of Lock Springs, *Steyermark 74203* (F). DeKalb Co., between Clarksdale and Bayfield, *Steyermark 14943* (MO). Franklin Co., Shaw Arboretum, Pinetum Lake, *Dille 436* (MO). Grundy Co., Oxbow Lake in bottoms of E side of Thompson River, 13 mi. SW of Trenton, *Steyermark 68498* (F). Henry Co., Big Creek, 3 mi. SE of Hartwell, *Steyermark 7542* (F). Iron Co., Iron Mountain Lake, 1924, *Kellogg s.n.* (MO). Jackson Co., Sibley, *Bush 4173* (GH, MO, NY, SMU, US). Jasper Co., near Waco, *Palmer 18476* (NY). Johnson Co., Bear Creek, 3.5 mi. E of Warrensburg, along Hwy. 50, *Steyermark 24543* (F, NY, TENN). Knox Co., bottom woods along old channel of Salt River, 1.5 mi. SW of Locust Hill, *Steyermark 70647* (F). Lewis Co., Mississippi River bottoms, E of Shiloh church, along Doe Run, 7 mi. N of Canton, *Steyermark 74081* (F). Lincoln Co., W Fork of Cuivre River, 5.5 mi. SW of Davis, *Steyermark 72351* (F). Linn Co., Locust Creek, Pershing State Park, 4 mi. SW of Laclede, *Steyermark 40422* (F, MO). Livingston Co., Shoal Creek, 1 mi. NE of Dawn, *Steyermark 68458* (F). Macon Co., Chariton River, 5 mi. NE of New Cambria, *Steyermark 40580* (F, MO, US). Montgomery Co., ca. 1 mi. W-SW of Wellsville, *Gereau & Gu 1190* (MO). Osage Co., along Gasconade River on SW side, 8 mi. SE of Linn, *Steyermark 79318* (MO). Randolph Co., Silver Spring Creek, 2 mi. S of Huntsville, *Steyermark 9349* (MO). Ray Co., 1892, *Bush s.n.* (MO, NY). St. Charles Co., 3 mi. E of St. Peters, *Bauer 701* (F). St. Louis Co., Mississippi River near Baden, *Steyermark 8751* (MO). Saline Co., along road leading to bridge over Blackwater River, Sect. 32, 5 mi. NW of Ridge Prairie, *Steyermark 21527* (F, MO). Schuyler Co., N side of Rt. 4, in bottoms of Chariton River, just inside Schuyler County, just E of Livonia, *Steyermark 70272* (F). Shelby Co., alluvial woods along NW side of Salt River, 3.5 mi. N of Shelbina, *Steyermark 66574* (MO). Vernon Co., Clear Creek, 4–5 mi. W of Virgil City, *Steyermark 9688* (F). NEVADA: Brown Co., Ainsworth, *Clements s.n.* (GH, NY, US). Cherry Co., Valentine Lakes Refuge, *Tolstead 411242* (MO). Colfax Co., 1 mi. S of Schuyler on Hwy. 15, along bank of Platte River, *Churchill 4224* (NY). Holt Co., Ewing, 1893, *Bates s.n.* (TEX). Madison Co., 4 mi. S of Norfolk, *Conard s.n.* (TENN, W). OHIO: Auglaize Co., S shore of Grand Lake St. Mary's, 0.1 mi. E of Auglaize–Mercer county line, ca. 4 mi. SW of the town of St. Mary's, 1967, *Stuckey s.n.* (GH, NY, US, VDB). Butler Co., Oxford, 1898, *Moseley s.n.* (F). Fulton Co., 0.5 mi. E of Brailey, 1927, *Moseley s.n.* (US). Gaillia Co., swamp along Rt. 35, 2 mi. S Rio Grande, *Bartley 2279* (US). Hamilton Co., Turkey Bottoms, 1905, *Braun s.n.* (US). Jackson Co., Hammertown Lake, *Bartley 3024* (NY). Lucas Co., Toledo, 1878, *Sanford s.n.* (GH). Paulding Co., ca. 0.5 mi. W of Mandale, *Stuckey 6267* (SMU). PENNSYLVANIA: Dauphin Co., ca. 2 mi. E-SE of Millersburg, *Berkheimer 14541* (CM). VIRGINIA: Buckingham Co., Sprouses Corner (near Dillwyn), *Bartley & Pontius 539* (NY). WISCONSIN: Brown Co., Fort Howard, Elmore's, 1881, *Schuette s.n.* (F, GH, NY). Columbia Co., Portage, 1892, *True s.n.* (GH). Crawford Co., Prairie du Chien, 1861, *Hale s.n.*(?). Dane Co., Madison, *Watson s.n.* (NY). Grant Co., Wyalusing State Park, *Musselman 3825* (NCU). Kenosha Co., along Lake Michigan, just N of Illinois state line and E of RR, *Iltis 20258* (MO). La Crosse Co., young mixed hardwood forest bordered by a steep rocky rip-rap bank on W and a stagnant backwater pool on E, *Swanson 1887* (MO, NY). Lincoln Co., *Seymour 16321* (GH, MO). Milwaukee Co., 1882, *Hasse s.n.* (NY). Monroe Co., Hwy. 21 near Wyeville, *Hartley 8222* (GH). Racine Co., *Hale s.n.* (NY, US). WEST VIRGINIA: Mason Co., Point Pleasant, *Bartley & Pontius 476* (NY). CANADA. ONTARIO: Essex Co., Sandwich, *Macoun 44462* (CM, GH, F); 1 mi. SW of Windsor, *Rogers 9687* (MSU); near Amherstburg, 1892, *Macoun s.n.* (GH, NY, US). Kent Co., 11 mi. W-SW of Cedar Springs, 4 mi. S-SE of Merlin, N side Lake Erie, *Fosberg 39627* (C). Lambton Co., Pt. Edward, Lake Huron, *Macoun 44461* (F, GH, NY); *s.c. 188* (MO). Welland Co., Port Colborne, 1937, *Allen s.n.* (NCU).

Ludwigia polycarpa is the only species in sect. *Microcarpium* that occurs consistently north of 37°N, in the central Midwest of the United States. The report of Kral (1976) on the range extension of *L. polycarpa* to Covington Co., Alabama (*Kral 40992*, FLAS, GH, MO, NCU, NY, US, USF, VDB), was based on a pure F_1 stand of natural hybrids between *L. pilosa* and *L. glandulosa*.

Ludwigia polycarpa is therefore effectively isolated geographically from all other species in the same section except *L. sphaerocarpa*, which has a wide distribution throughout the Atlantic and Gulf coastal plains, also with scattered populations in the northeastern states as well as around the southern border of Lake Michigan (Fig. 45). Indeed, natural hybridization takes place where geographical isolation is not maintained, as is evidenced by the presence of fertile hybrid populations of *L. polycarpa* × *L. sphaerocarpa* found in Starke Co., Indiana (Peng, 1988). Furthermore, sterile, intersectional hybrids between *L. polycarpa* and the prostrate, opposite-leaved *L. palustris* (sect. *Dantia*), which is very widespread throughout the eastern half of the United States, are found in Ballard Co., Kentucky, the southern border of the range of *L. polycarpa* (Peng, 1988).

Herbarium specimens of *Ludwigia polycarpa* are rarely misidentified due partly to its geographical isolation and partly to its distinctive morphology. Plants of *L. polycarpa* are generally uniform and are characterized by having densely minutely papillose-serrulate leaf margins, elongate-acuminate sepals with reflexed tips, long bracteoles (3.5–6.5(–8) mm) attached above the capsule base, and the oblong-obovoid capsules that frequently exhibit reticulate markings along the rounded corners.

Plants of *Ludwigia polycarpa* produce stolons

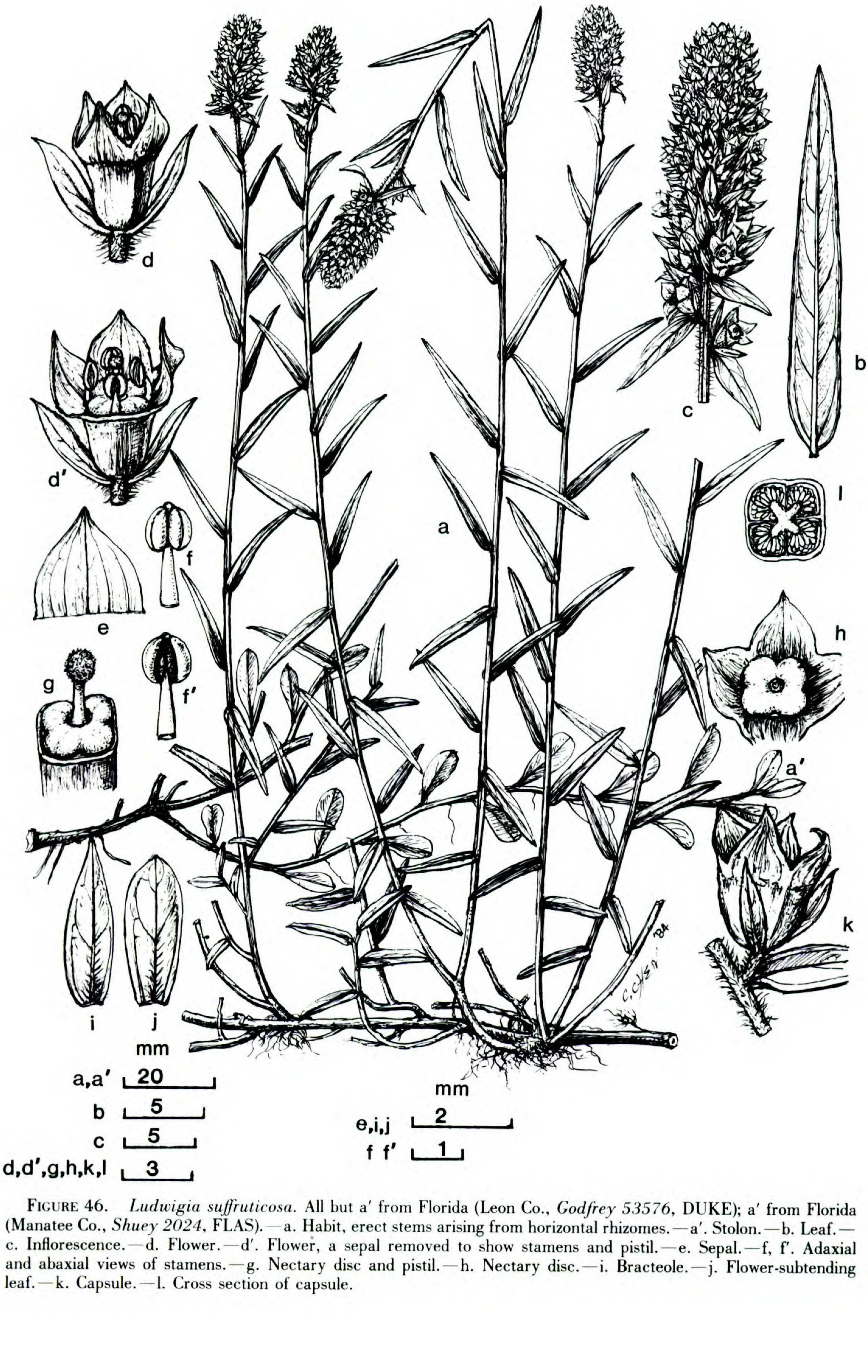

FIGURE 46. *Ludwigia suffruticosa*. All but a′ from Florida (Leon Co., *Godfrey 53576*, DUKE); a′ from Florida (Manatee Co., *Shuey 2024*, FLAS).—a. Habit, erect stems arising from horizontal rhizomes.—a′. Stolon.—b. Leaf.—c. Inflorescence.—d. Flower.—d′. Flower, a sepal removed to show stamens and pistil.—e. Sepal.—f, f′. Adaxial and abaxial views of stamens.—g. Nectary disc and pistil.—h. Nectary disc.—i. Bracteole.—j. Flower-subtending leaf.—k. Capsule.—l. Cross section of capsule.

from their lower nodes in late flowering season, like other species do. Their stolons, however, are much shorter, normally up to 15 cm, and their leaves, unlike those of any other species of sect. *Microcarpium*, are often densely congested and overlap at the apex of the sparsely leaved stolons. The modified stolon is comparable to the perennating turion of *Epilobium* (Keating et al., 1982), which apparently serves as an adaptation to the severe winter that plants of *L. polycarpa* have to endure in the northern states.

The short stolons are occasionally found growing from the nodes of aerial stems that have fallen to the ground. Such specimens include:

U.S.A. ILLINOIS: Riverside, *1886, Ohlendorf s.n.* (F): Western Springs, *Smith 676* (F). MISSOURI: Saline Co., Blackwater River, Sect. 32, 5 mi. NW of Ridge Prairie, *Steyermark 21527* (MO).

6. Ludwigia suffruticosa Walter, Fl. Carol. 90. 1788. *Isnardia suffruticosa* (Walter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. *Ludwigia capitata* Michaux, Fl. Bor.-Am. 1: 90. 1803, nom. illegit., based on *L. suffruticosa* Walter. *Isnardia capitata* (Michaux) DC., Prodr. 3: 60. 1828. TYPE: U.S.A., "the Carolinas," s.d., *T. Walter* (type not seen, not located at BM). Figure 46.

Plants bearing rhizomes and stolons. Stems erect, unbranched or slightly branched, (16–)30–90 cm tall, glabrous except for the rachis and stem base, these often puberulous to densely hirtellous, the hairs 0.2–0.6(–0.8) mm long, aerenchyma in the lower part very rarely seen. Rhizomes 1–several, 6–55 cm long, 1.25–4.5 mm thick, often branched, glabrous to densely hirtellous, the leaves dark purplish, minute, scalelike, oblate or suborbicular, ca. 0.3–0.6 mm long, 0.6–0.9 mm wide, appressed. Stolons less commonly seen than rhizomes, 8–80 cm long, 1.1–2.2 mm thick, branched, glabrous to densely hirtellous, the leaves purplish, oblong or oblanceolate-elliptic to spatulate, 4–35 mm long, 1.6–15 mm wide, glabrous to pilose, the petioles 1–6 mm long. Cauline leaves green, lance-elliptic, lance-linear to linear, the lower ones shorter, oblong-oblanceolate to oblong or oblong-lanceolate, 25–95 mm long, (1–)3–9 mm wide, glabrous to ± pilose on those at stem base/peduncles, the apex manifestly elongate tapering into a sharp point or acute on lower leaves, the margin entire, hydathodal glands usually obscure, submarginal veins parallel to the midvein often prominent on the abaxial surface, the base rounded or obtuse, sessile. Stipules deltoid, 0.25–0.45 mm long, 0.15–0.4 mm wide. Flowers in racemose inflorescence 1–5(–12) cm long, 1–2 cm wide, terminal on the stems or branches; the subtending leaves much reduced and bractlike, lanceolate or lance-elliptic, 4–12(–18) mm long, 1.35–3.5(–4) mm wide, glabrous to hirtellous along margin and venation of the abaxial surface, especially on the lower half. Sepals whitish, broadly ovate or deltoid, ascending, 2.3–3.5(–4) mm long, 2.3–3.2(–3.8) mm wide, glabrous, apex acuminate, margin entire, base connate 0.6–1 mm above the ovary. Petals 0. Anthers 0.75–1(–1.3) mm long; filaments pale yellowish, 1.2–2 mm long, distinctly dilated toward the base. Pollen grains shed as tetrads. Nectary disc yellowish, raised 0.5–0.6 mm on top of the ovary, 1.8–3.1 mm across, the lobes obscure, glabrous. Style pale yellowish, 0.9–1.7 mm long, glabrous; stigma whitish, 0.4–0.75 mm long, 0.5–0.75 mm thick, distinctly 4-lobed on the apex. Capsules broadly obpyramidal with rounded corners, sometimes subspherical, 2.5–4.25 mm long, 2.5–4.5(–5) mm thick, glabrous or in a few cases minutely strigillose, the hairs ca. 0.05–0.1 mm long, pedicels 0.5–1.5(–2) mm long. Bracteoles flanking capsule base or on the short pedicel, 3.5–5(–6) mm long, (1.2–)1.4–2 mm wide, glabrous to pilose without, glabrous within. Seeds brown, elliptic oblong, curved on both ends, 0.5–0.6 mm long, 0.2–0.25 mm thick, surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. suffruticosa* grow in sandy ditches, along river marshes, in meadows, in limestone sinks, in cypress swamps, and in moist pinelands. This species occurs along the Atlantic coast from southeastern North Carolina through eastern South Carolina, southern Georgia, and throughout the northern three-quarters of the Florida peninsula. To the west this species occurs through most of the Florida panhandle, extreme southeastern Alabama, and southern Georgia (Fig. 47). Flowering from May to September; fruiting from June to October.

Representative specimens examined. U.S.A. ALABAMA: Houston Co., Indigo Pond, SW of Cottonwood, *Kral 43405* (ENCB, MO, US, VDB). FLORIDA: Alachua Co., Gainesville, E of airport, 1937, *Murrill s.n.* (DUKE, MO). Bay Co., just S of Bay–Washington county line, *Adams 697* (DUKE, FLAS, FSU, GH, NCU, SMU, VDB). Bradford Co., Sampson City, 1946, *Dennison & Arnold s.n.* (FLAS). Brevard Co., N side of Cocoa, *Kral 5484* (NCU, NO, SMU). Charlotte Co., Caloosa Experimental Range, US Forest & Range Station, *Adams 235* (FSU, GA, GH). Citrus Co., 5 mi. S of Homosassa, *Kral 7771* (GA). Clay Co., Lake Brooklyn beside FL Hwy. 21, *D'Arcy 953* (C, FLAS). Collier Co., near Immokalee, *Craighead s.n.* (USF). Columbia Co., Lake City, 1893, *Rolfs s.n.*

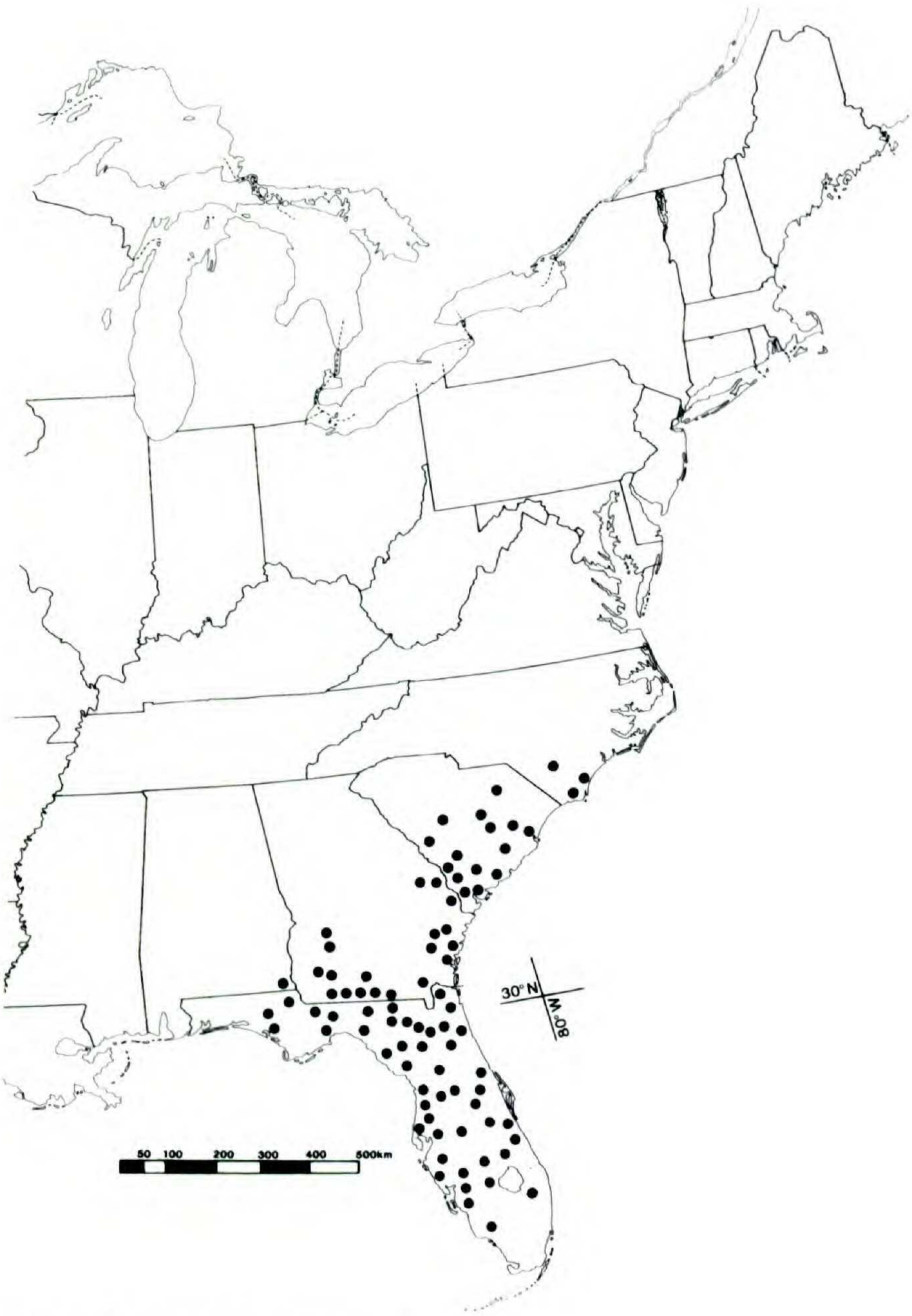

FIGURE 47. Distribution of *Ludwigia suffruticosa*.

(GA). De Soto Co., 4 mi. W-NW of Arcadia, *Kral 17965* (VDB). Dixie Co., 3.5 mi. N of Hines, 1937, *Pasture Survey s.n.* (FLAS). Duval Co., near Jacksonville, *Curtiss 5135* (GA, GH, JE, MSC, NY, US, W). Gadsden Co., 2.4 mi. N of Woodville, E side of US Hwy. 319, *Dress & Read 7736* (AAU, CAS). Gilchrist Co., 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Glades Co., 6.4 mi. SE of jct. of FL Hwy. 29 and US Hwy. 27, *Raven 18678* (DS). Hamilton Co., 5 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Hernando Co., *Cooley et al. 7068* (NCU, USF). Highlands Co., 10 mi. S of Lake Placid, *Brass 15203* (FLAS, GH, USF). Hillsborough Co., 1.5 to 1.7 mi. S of FL Hwy. 674 on the E side of Taylor Grill Dr., *Peng et al. 4327* (MO). Indian River Co., near Eau Gallie, *Curtiss 927* (CM, F, FLAS, GA, MO, NCU, NY, US). Jackson Co., near Dellwood, along FL Hwy. 69, *Hood 2759* (FLAS). Lake Co., vicinity of Eustis, *Nash 950* (F, GH, MO, MSU, NY, US). Lee Co., *Hitchcock 118* (F, GH, MO, NY, US). Leon Co., 6 mi. S of Tallahassee, *Godfrey 53576* (DUKE, FLAS, NY, SMU, USF, VDB). Levy Co., 5 mi. SE of Lebanon Station, *Kral 7807* (GA). Madison Co., 4 mi. N of Greenville on FL Hwy. 221, *Ramsey 104* (FSU, NCU, US). Manatee Co., 6.7 mi. W of jct. of FL Hwys. 64 and 675, E of Bradenton, *Perdue 1779* (C, FSU, GA, GH, LL, NCU, SMU, USF). Marion Co., Lake Kerr, 1935, *West & Arnold s.n.* (FLAS). Martin Co., Jonathan Dickinson State Park, W of Pinegrove Campground, *Popenoe 351* (FTG). Nassau Co., ca. 7 mi. SE of Yulee, *Kral 18629* (VDB). Okeechobee Co., US Hwy. 441, 20 mi. E of Kenansville, 1 mi. S of Osceola Co. line, *Clark 3477* (Duke). Orange Co., 5 mi. S of Oakland, *Kral 7735* (FLAS, GA, GH, US, USF). Osceola Co., W side of main road leading S through Poinciana S of US hwys. 17 & 92, *Wunderlin & Shuey 5779* (TENN, USF). Palm Beach Co., 2.0 mi. W of Lantana, *Howard 12960* (C, DS, DUKE, FLAS, GA, GH, MO, MSC, NO, NY, S, SMU, TENN, TEX, U, US, W). Pasco Co., 10 mi. E of Zephyrhills, *Kral 7264* (GH, NY, USF). Pinellas Co., FL Power right-of-way, Hwy. 19, 1 mi. N of Hwy. 588, *Genelle & Heming 2865* (TENN, USF). Polk Co., SE of Hesperides, ca. 8 mi. E of Lake Wales, off FL Hwy. 60, *Lakela 24806* (DS, USF). Putnam Co., *Martin & Copper 110* (FLAS, USF). St. Johns Co., Palm Valley, 1951, *Buker s.n.* (CM). Sarasota Co., 7 mi. N of S entrance of park, Myakka region, *Dodson 4515* (USF). Seminole Co., Prairie Lake, *Schallert 15229* (AAU, JE, U, WAG). Sumter Co., 3 mi. SW of Tarrytown, *Kral 7925* (FLAS, GH, USF).

Suwannee Co., 4 mi. E of Wellborn, *Wiegand & Manning 2202* (GH). Taylor Co., 3.2 mi. N of Shady Grove, *Raven 18619* (DS, NCU). Union Co., 1 mi. E of Worth Springs, *Murill 775*(?). Volusia Co., 3 mi. N-NW of DeLeon Springs, *Kral 1699* (CA, GH, USF, VDB). Wakulla Co., 0.5 mi. N of Ochlockonee River on US Hwy. 98, *Kral 3027*(?). Washington Co., 6 mi. S of Wausau, *Webster & Wilbur 3622* (GH, NY, SMU, US). GEORGIA: Baker Co., ca. 8 mi. SE of Milford, *Kral 20493* (VDB). Brooks Co., 12.5 mi. SE of Quitman, *Faircloth 3338* (GA, MO, NCU). Charlton Co., between Folkston and Mattox, *Correll 5517* (DUKE, FSU, GA, TENN). Cook Co., 7.6 mi. SE of Adel, *Faircloth 2927* (GA, NCU). Echols Co., 5.5 mi. S of Stockton on US Hwy. 129, *Norsworthy 162* (MO, NCU). Effingham Co., near Luciene Bay, *Eyles 6376* (GA). Glynn Co., St. Simons Island, 1946, *Ford & Thorne s.n.* (TENN). Grady Co., Susina Plantation, *White 180* (FSU). Jenkins Co., 2.5 mi. N of Millen, *Pyron & McVaugh 919* (GA). Lee Co., ca. 7 mi. N of Leesburg, *Cronquist 5445* (FLAS, GA, GH, MO, NY, SMU, US). Liberty Co., 7 mi. NE of Hinesville, *Wiegand & Manning 2201* (GH). Long Co., 3.8 mi. E-SE of Long–Tattnall county line on GA Hwy. 196 near RJ with GA Hwy. 261, *Faust & Jones 19981* (FSU, GA, VDB). Lowndes Co., 9.5 mi. SE of Valdosta, intersection of Southern RR and Howell Hwy., *Faircloth 2887* (GA, NCU). McIntosh Co., 1.8 mi. S-SW of N tip of Sapelo Island, *Duncan 20406* (CAS, DUKE, F, FLAS, GH, MISS, NCU, SMU, TENN, TEX, US, USF). Mitchell Co., *Duncan 6682* (GA). Screven Co., W of Blue Springs, *Duncan 5581* (GA, TENN). Sumter Co., S of Leslie, *Harper 484* (F, GH, MO, MSC, NCU, NY, S, US). Wayne Co., SE of Lindy's Bluff NE of Jesup, *Duncan 3759* (FLAS, GA, MISS, SMU, US, USF). NORTH CAROLINA: Brunswick Co., ca. 2 mi. W of NC Hwy. 133 off Co. Rd. 1536, Boiling Springs, *Bradley & Stevenson 3308* (BOON, C, ECUH, MEX, MISS, S, TEX, UNA, U, US, USCH, WCUH). Bladen Co., 2.5 mi. E of Elizabethtown, *Godfrey & Fox 49485* (DUKE, FSU, MO, NCSC, NY). New Hanover Co., Fort Fischer on the lower Cape Fear Peninsula, *Godfrey 4698* (GH, NLSC, NY, US). Orange Co., Taft, *Schallert 15229* (M). SOUTH CAROLINA: Aiken Co., Savannah River Plant, Ellington Bay, 1975, *Shealy s.n.* (USCH). Allendale Co., SE of Barton, *Ahles & Bell 15855* (CM, NCU). Bamberg Co., 1 mi. E of jct. of Co. Hwy. 59 and US Hwy. 601 on Co. Hwy. 59, S-SE of Bamberg, *Ahles & Haesloop 30589* (NCU). Beaufort Co., Bluffton, 1887, *Mellichamp s.n.* (US). Berkeley Co., 1 mi. N of Russelville, *Martin 48* (DUKE, GA, NY, TENN, US). Charleston Co., Adams Run, *Godfrey & Tryon 1565* (GA, NY, US). Clarendon Co., 1 mi. W of Davis Station, *Radford 28239* (FLAS, NCU, SMU). Colleton Co., E side of Walterboro, *Kral 19202* (VDB). Darlington Co., Hartsville, 1908, *Coker s.n.* (NCU, NY). Georgetown Co., 9 mi. N of Georgetown, *Godfrey & Tryon 337* (DUKE, F, GH, MO, NY, US). Hampton Co., 0.2 mi. N of Luray on US Hwy. 321, *Bell 5044* (USF). Jasper Co., NW of Tillman, *Ahles & Williamson 54838* (NCU). Lexington Co., Columbia, *Godfrey & Tryon 1241* (GH, US). Sumter Co., 1884, *Smith s.n.* (F, GH, US). Williamsburg Co., 6 mi. N of Kingstree, *Wiegand & Manning 2200* (GH).

Ludwigia suffruticosa is a very distinct species that has many features unique within sect. *Microcarpium*. Its leaves are rounded to obtuse at the base and clearly sessile. It has a very compact, racemose inflorescence at the very top of each erect stem, as is suggested by the name "*Ludwigia capitata*," an illegitimate synonym of *L. suffruticosa* Walter, coined by Michaux (1803). The stems are usually single or occasionally with one or two or more branches arising directly beneath the main inflorescence. These branches always rise above the main inflorescence and are each terminated by a smaller compact raceme. Furthermore, each flower is usually subtended by a reduced, bractlike leaf in addition to the bracteoles that flank the ovary. It is also the only species in sect. *Microcarpium* that perennates mainly by underground rhizomes. Stolons that float or send roots into mud, prevalent in many other species, are not common in *L. suffruticosa*. It is especially peculiar in having variously pubescent inflorescences and lower stems, stolons, and underground rhizomes but is otherwise completely glabrous in the middle—see below.

The flowers of this species are characteristically very compactly arranged into a raceme up to 5 cm long. The following specimens examined, however, have less compact and longer inflorescences but are otherwise typical of *Ludwigia suffruticosa*:

U.S.A. FLORIDA: Charlotte Co., Caloosa Forest/Expt. Area, Pasture 8, *Parrott 219* (DUKE, inflorescences 7 cm long). Hillsborough Co., Tampa, Gates Dr., in sandy field W of Gates Apts., *Dille 424* (MO, inflorescences up to 12 cm long, co-occurring with normal, compact-inflorescenced individuals (same locality, *Dille 423*, MO). GEORGIA: Wayne Co., in very sandy soil SE of Lindy's bluff, just NE of Jesup, *Dunkan 3759* (GH, inflorescences 8 cm long; NCU, inflorescences 10.5 cm long).

The distribution pattern of pubescence in plants of *Ludwigia suffruticosa* is peculiar and variable. The plants range from being completely glabrous to densely, minutely hirtellous with multicellular hairs up to 0.6(–0.8) mm long on rhizomes, stolons, stolon leaves, stem base, and basal leaves of the lower plant body and peduncles, pedicels, flower-subtending leaves, and bracteoles of the upper part but are completely glabrous in the middle part of the plant body. The capsules are usually completely glabrous. In the following specimens, however, erect, microscopic protuberances ca. 0.02–0.1 mm long are found evenly but not densely distributed on the fruit wall:

U.S.A. FLORIDA: Gilchrist Co., in swamps 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Hillsborough Co., Tampa, Gates Dr. in sandy field W of Gates Apts., *Dille & Dille 424* (MO); in wet ground along SR-581, ca. 5 mi. N of Tampa, *Funk 72*; *Gregory 46*; *Kuczynski 48*; *Robbins 130*; *Rose 11*; *Willett 10* (all USF). Leon Co., bordering Lake Jackson on NW side, just N of route

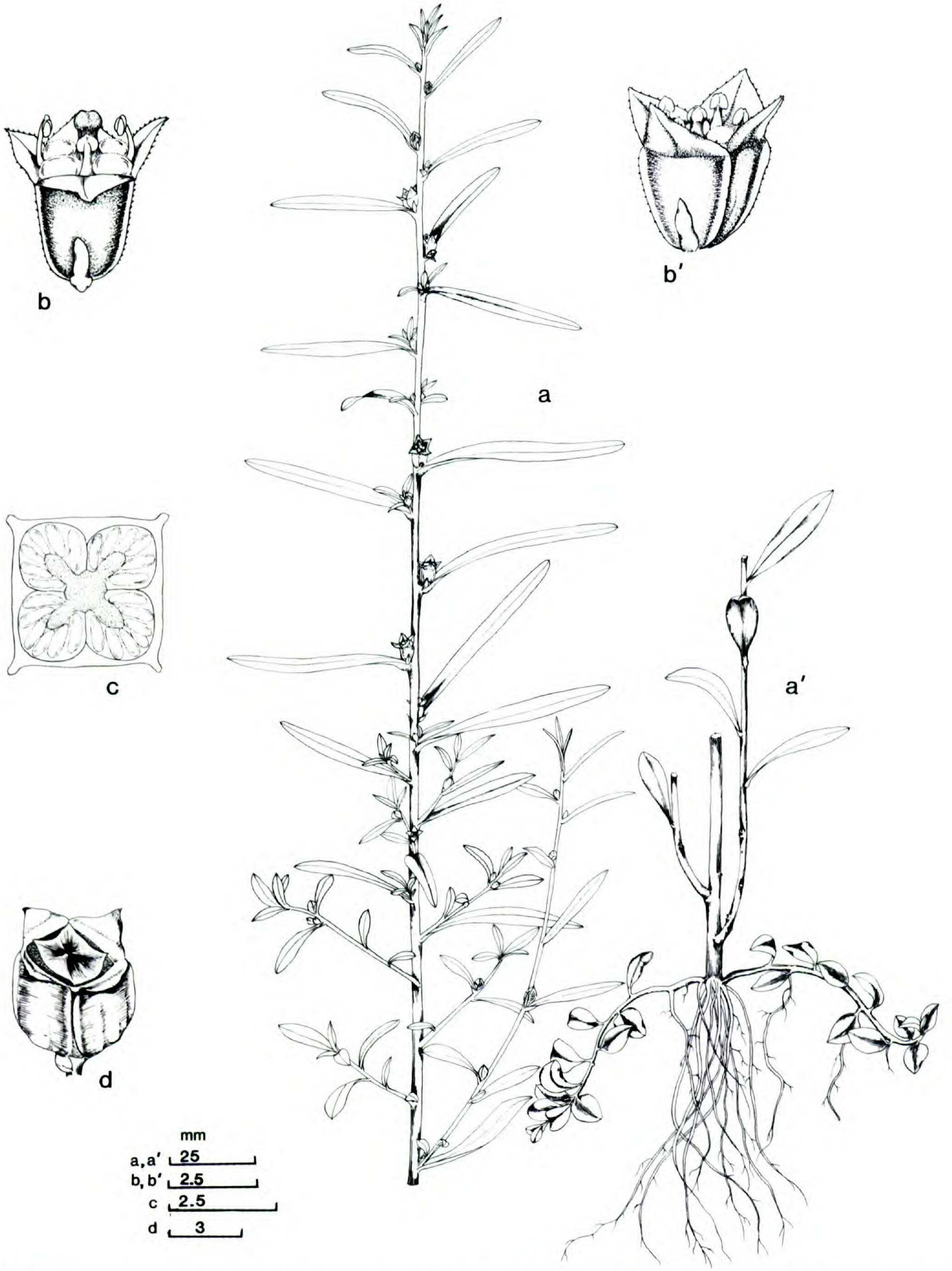

FIGURE 48. *Ludwigia lanceolata* (Florida: Highlands Co., *Peng et al. 4193*, MO).—a. Habit, erect stem.—a′. Stem base with stolons.—b, b′. Flower.—c. Cross section of capsule.—d. Dehiscent capsule.

27, NW of Tallahassee, *Anderson 4497* (GA, MO); on FL 363, 3 mi. N of Woodville, *Dille & Dille 421* (MO); Lake Jackson, adjacent to US 27, *Faircloth 246* (MO, NCU); shores of small pond, 6 mi. S of Tallahassee, *Godfrey 53576* (DUKE, FLAS, NCU, NY, SMU, USF, VDB); wet sands, exposed shores of sinkhole pond, by Spring Hill Rd., S of Tallahassee, *Godfrey 76066* (FSU); along US 319, ca. 5 mi. S of Tallahassee, *Henderson 63-1683* (TEX); margin of a small lake, along FL 271, ca. 5 mi. S of Tallahassee, *Henderson 67-1455* (VDB); near Lake Jackson, 8 mi. NW of Tallahassee, 1940, *Hocking s.n.* (FLAS). Orange Co., *Godfrey 57330* (FSU).

Polk Co., margin of a small lake, SE of Hesperides, ca. 8 mi. E of Lake Wales, off number 60, *Lakela 24806* (DS).

In a specimen collected from Florida (Leon Co., 4 mi. S of Tallahassee, on Rt. 369, 1950, *Sargent s.n.* (GA)) the capsule wall is minutely pilose with hairs ca. 0.4 mm long.

The sepals of *Ludwigia suffruticosa* are normally glabrous, but in the following specimen the sepals are minutely pilose:

U.S.A. FLORIDA: Duval Co., vicinity of Mayport & Jacksonville, 1870–1876, *Keeler s.n.* (NY).

Ludwigia suffruticosa, *L. alata*, *L. pilosa*, and *L. sphaerocarpa* are the species in sect. *Microcarpium* that do not undergo mechanical self-pollination. With its whitish creamy sepals, which are very showy in the dense flower aggregates, the cross-pollinating *L. suffruticosa* successfully attracts many insects, mostly bumblebees, honeybees, and wasps. It occurs with at least four species of *Ludwigia* (*L. alata*, *L. linearis*, *L. lanceolata*, and *L. pilosa*) in the field, hybridizing with all but *L. linearis*. These results are mirrored in the biosystematic study (Peng, 1988): artificial hybrids between *L. linearis* and *L. suffruticosa* are weak and inviable, whereas the other combinations that occur in nature have been synthesized successfully and were very vigorous in the experimental greenhouse.

Remarks on natural hybrids between *Ludwigia suffruticosa* and either *L. alata* or *L. lanceolata* are provided in the accounts of *L. alata* and *L. lanceolata*. Natural hybrid populations of *L. suffruticosa* × *L. pilosa* have previously been given a varietal status within *L. suffruticosa* (as *L. capitata* Michaux *β pubens*) by Torrey & Gray (1840), which was subsequently and incorrectly considered to be a synonym of *L. pilosa* by Munz (1944, 1965). The hybrids are densely hirtellous throughout, but the hairs are not as long as those of *L. pilosa*, and the sepals are neither cuspidate nor elongate-acuminate, but rather acuminate. Further, their stems are not well branched, their leaves are often long and narrow, their flowers are in more or less congested racemes on the upper part of the stem or branch, and the leaves that subtend their flowers are slightly reduced and bractlike. The combination of these characteristics clearly suggests that such plants represent hybrid populations of *L. suffruticosa* × *L. pilosa*. The possibility that *L. ravenii*, the only species other than *L. pilosa* that is consistently densely hirtellous, was involved in their parentage is reduced because it is rare and not known to occur with *L. suffruticosa*. Furthermore, the seed surface of the hybrid plants consists of subisodiametric cells, a characteristic of both *L. suffruticosa* and *L. pilosa*, but not of *L. ravenii*.

7. Ludwigia lanceolata Elliott, Sketch Bot. S.C. & Ga. 1: 213. 1817. *Isnardia lanceolata* (Elliott) DC., Prodr. 3: 61. 1828. TYPE: U.S.A. Georgia: in swamps, s.d., *J. E. Leconte s.n.* (holotype, CHARL; photographs, GH, MO; isotypes, P, PH). Figure 48.

Plants glabrous. Stems often brownish purple, erect, leafless below, branched above, 45–100 cm tall; aerenchyma well developed in lower stems when submersed in water; leaf bases slightly decurrent along the stems. Stolons up to 40 cm long, 2 mm thick, the leaves remote, 1–3 cm apart, purplish, rotund or elliptic to broadly elliptic, 5–27 mm long, 6–12 mm wide, apex rounded, obtuse or acute, base attenuate into winged petioles 2–10 mm long. Cauline leaves dark green, the lower ones sometimes purplish, leaves on the main stem elliptic, oblanceolate or narrowly oblanceolate, those on the branches usually much reduced, ranging from narrowly elliptic to very narrowly elliptic or linear; in general, leaves 20–75 mm long, 2–7.5 (–14) mm wide, apex acute to narrowly acute, margin entire with minute hydathodal glands, base narrowly cuneate or sometimes attenuate into a winged petiole up to 5 mm long. Stipules dark reddish purple, ovate to very widely ovate, succulent, 0.2–0.45 mm long, 0.15–0.25 mm wide. Flowers in upper leaf axils. Sepals greenish, shallowly triangular or deltate, ascending, 1.5–2.5 mm long, 1.8–3.3 mm wide, glabrous, apex acute to acuminate, minutely papillose along the margins. Petals 0. Anthers 0.4–0.6(–0.75) mm long; filaments nearly translucent, 1–1.4 mm long, dilated toward the base. Pollen grains shed as tetrads. Nectary disc yellowish green, raised 0.4–0.6 mm on ovary apex, 1.75–2.6 mm across, 4-lobed, glabrous. Style yellowish green, 0.5–0.7 mm long, glabrous; stigma yellowish, subglobose, 0.3–0.5 mm long, 0.7–1 mm thick. Capsules obpyramidal, winged on the corners, 3.5–5 mm long, 2.5–4.5 mm thick (as measured from wing to wing), glabrous, occasionally minutely strigillose, the wings 0.3–0.7 mm wide, usually minutely strigillose; pedicels up to 0.5 mm long. Bracteoles located at or slightly above capsule base and on 2 sides, variable in shape and size even in the same plant, ovate-elliptic to very narrowly elliptic, 1.5–4.3 mm long, 0.4–1.4 mm wide, margin minutely papillose, often with a distinct, rounded, swollen tissue 0.5–1 mm

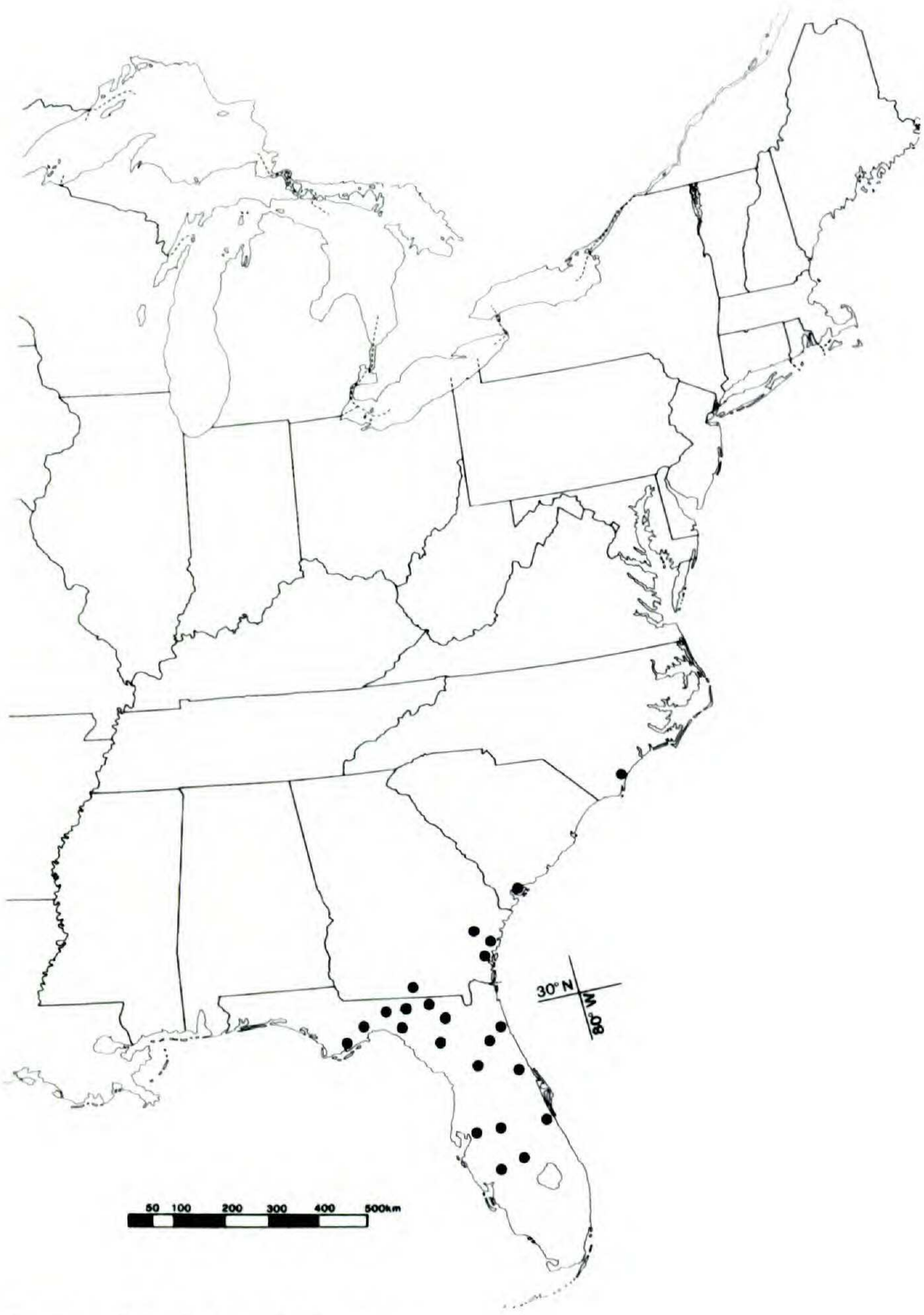

FIGURE 49. Distribution of *Ludwigia lanceolata*.

across below the point of attachment. Seeds light brown, narrowly oblong with constricted ends, 0.65–0.75 mm long, 0.25–0.3 mm wide, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia lanceolata* grow in ditches, low meadows, cypress swamps, moist pinelands, edges of pocosins, and on sandy peaty soil. This is a fairly uncommon species, with scattered populations occurring along the Atlantic coast of southern North Carolina, South Carolina, eastern and southern Georgia, and the Florida peninsula. This species reaches its western limit in the central panhandle of Florida (Fig. 49). Flowering from June to October; fruiting from June to November.

Representative specimens examined. U.S.A. FLORIDA: Brevard Co., Okeechobee region, *Fredholm 5987* (GH, MO, NY, US). Columbia Co., Lake City, *Nash 2502* (E, F, GH, MO, MSU, NY, US). De Soto Co., 5 mi. N of Arcadia, 1938, *West s.n.* (FLAS). Franklin Co., Apalachicola, *Chapman 4177* (GH, MO, NY, US, W). Gilchrist Co., 5 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Hamilton Co., Cypress Swamp, 6 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Highlands Co., on Co. Rd. S-634, 1 mi. W of US Hwys. 27 & 98, *Peng et al. 4183* (MO). Hillsborough Co., 1.5 to 1.7 mi. S of Hwy. 674, on E side of Taylor Gill Dr., *Peng et al. 4326* (MO). Jefferson Co., vicinity of Lloyd, *Godfrey & Houk 61411* (FSU). Madison Co., 8 mi. W of Greenville, *Kral 3741* (FSU, NY, USF). Marion Co., W of Lake Ocklawaha, *Martin & Cooper 877* (FLAS). Polk Co., 4.5 mi. E of Haines City, on FL 580, 1963, *Conard s.n.* (GH). Putnam Co., Fowlers Lake, 1935, *Weber s.n.* (FLAS). St. Johns Co., 5 mi. W of St. Augustine, *Godfrey & Reinert 61185* (FSU). Taylor Co., 1.2 mi. SE of Salem, *Godfrey 64738* (DS, FSU, LL, NCU). Volusia Co., ca. 4 mi. S jct. state 44 & 415, *Kral 18435* (VDB). Wakulla Co., Cow Swamp, Apalachicola National Forest, NW of Crawfordville, *Godfrey 64876* (FSU). GEORGIA: Glynn Co., St. Simons Isl., *Ford & Thorne 2788* (TENN). Long Co., 5 mi. W off US 301, on Hughes River Rd., *Bozeman & Radford 2042* (NCU). Lowndes Co., pine-barren pond S of Melrose, *Harper 1605* (E, F, GH, MO, MSU, NCU, NY, US). McIntosh Co., 1.25 mi. N of Fort Barrington,

TABLE 5. Comparison of *Ludwigia alata* with *L. lanceolata*.

Characters	*L. alata*	*L. lanceolata*
Stems	Often winged, sometimes obscurely so	Nearly smooth
Sepal		
Color	Whitish adaxially	Greenish adaxially
Length	Subequal to capsule	Shorter than capsule
Anther length (mm)	0.55–0.9	0.4–0.6(–0.75)
Filament length (mm)	1.1–1.7	1–1.4
Pollen grains shed	Singly	In tetrads
Nectary disc width (mm)	2–3.3	1.75–2.6
Style length (mm)	0.8–1.3	0.5–0.7
Breeding system	Obligate outcrossing	Modally autogamous
Capsule wall between the winged corners	Bulging out longitudinally in the central part	Smooth
Seed length/width ratio	Ca. 2	Ca. 2.4–2.8
Surface cells	Columnar	Suborbicular
Chromosome number	$n = 24$	$n = 16$

Cox Road, *Bozeman 2176* (FLAS, GA, NCU). NORTH CAROLINA: New Hanover Co., near Wilmington, 1867, *Canby s.n.* (NY). SOUTH CAROLINA: Beaufort Co., Bluffton, *Mellichamp s.n.* (NY).

Ludwigia lanceolata is interfertile with all seven other tetraploid members of sect. *Microcarpium*. However, it is most similar to the hexaploid *L. alata* in general aspects and fruit morphology, and is suspected to have been one of the parents of that species (Peng, 1988). For a detailed discussion of these two species, see remarks under *L. alata* and Table 5.

Ludwigia lanceolata has been found growing with *L. pilosa*, *L. suffruticosa*, both tetraploids, and with the diploid *L. linearis*. *Ludwigia alata* and *L. lanceolata* have not been found growing together, although they have overlapping ranges in the eastern and central Florida panhandle. It is worth noting that, although both species occur in generalized, wet habitats, such as the borders of ditches, ponds, and swamps, *L. lanceolata*, unlike *L. alata*, is not found in the limestone prairies and brackish marshes that prevail in the Everglades region of southern Florida. No hybrids have been observed, but they would be very difficult to detect without measuring pollen stainability or determining chromosome numbers.

Ludwigia lanceolata intergrades with *L. pilosa*, and fertile hybrids between them are frequent in nature. Such hybrids were named *L. simulata* by Small (1903). The type at NY (West Florida, *Biltmore Herbarium*) shows a combination of densely strigillose hairs and four-angled or barely winged capsules; it apparently arose following hybridization between a parent with strongly winged capsules (*L. alata* or *L. lanceolata*) and one that was pubescent (*L. pilosa*, *L. ravenii*, or *L. sphaerocarpa*). The isodiametric seed surface cells, combined with the fact that these plants shed their pollen grains as tight tetrads clearly suggest *L. lanceolata* and *L. pilosa* as the parents. Two other collections identified as this hybrid are also from Florida:

U.S.A. FLORIDA: Franklin Co., Apalachicola, *Chapman s.n.* (F, US). Highlands Co., Bear Point, Lake Childs, *Brass 15532* (GH, US).

Ludwigia lanceolata also intergrades with *L. suffruticosa*. For example, putative parents and introgressed hybrid populations were found in the same sandy ditch by a prairie in Hillsborough Co., Florida (*Peng 4324*, *4328*, MO). The leaves of the hybrids were narrow like those of *L. suffruticosa*, but the stems were well branched above the middle. The flowers are produced in somewhat congested racemes at the top of each branch, and the capsules were obpyramidal and weakly four-angled. *Peng 4324* had 85% stainable pollen and formed 16 bivalents in meiosis.

8. Ludwigia alata Elliott, Sketch Bot. S. C. & Ga. 1: 212. 1817. *Isnardia alata* (Elliott) DC., Prodr. 3: 61. 1828. LECTOTYPE: U.S.A. South Carolina: Charleston Co., found in damp places on Sullivan's Island, in the wooded part of the island, July–Sep., s.d., *S. Elliott s.n.* (PH; no authentic material found in Elliott's herbarium at CHARL, so sheet from PH selected as lectotype). Figure 50.

Plants glabrous. Stems erect or somewhat sprawling, 40–120(–160) cm tall, branched above, aerenchyma distinct in lower parts when sub-

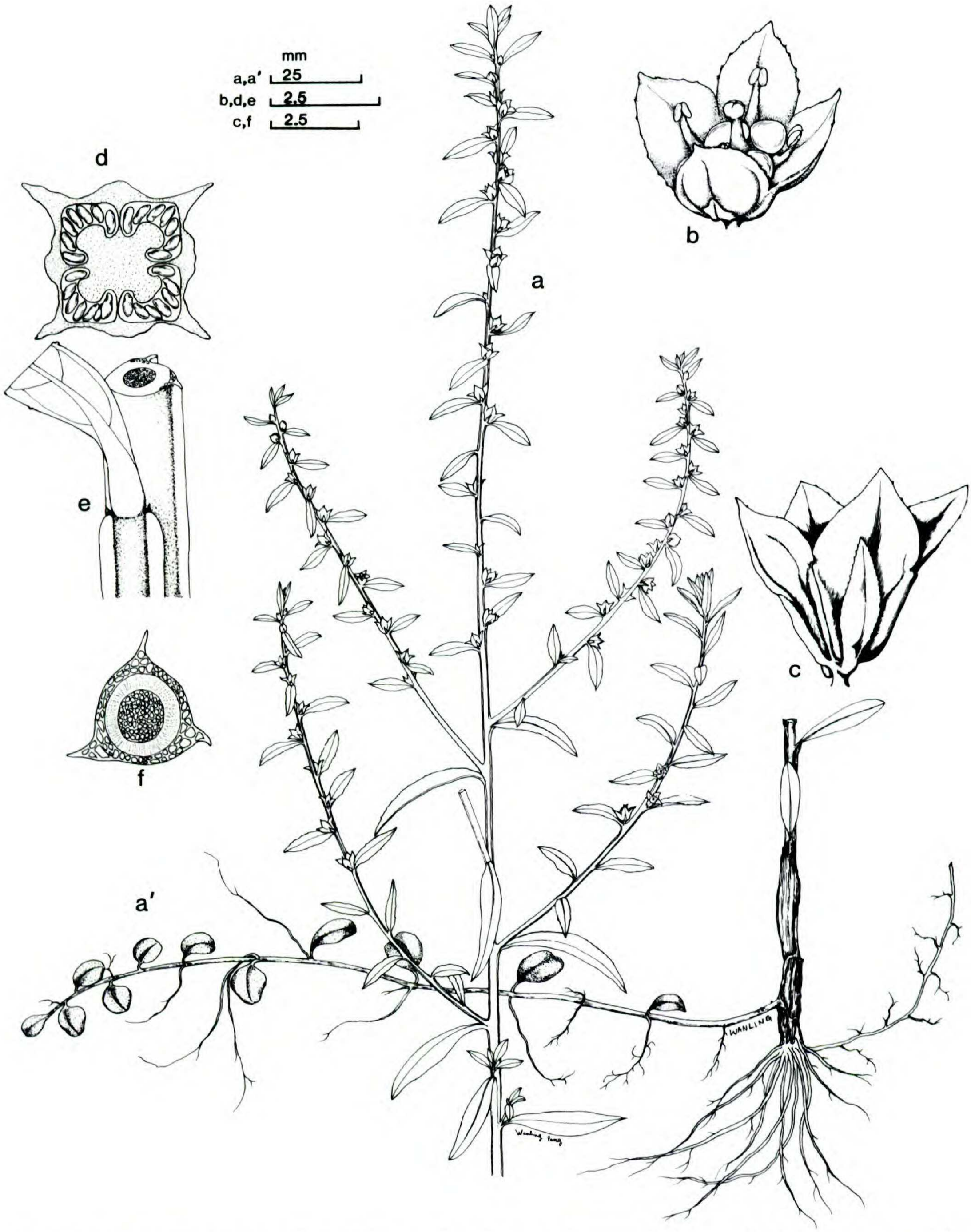

FIGURE 50. *Ludwigia alata* (Florida: Martin Co., *Peng et al. 4203*, MO).—a. Habit, erect stem.—a'. Basal stolon.—b. Flower.—c. Capsule.—d. Cross section of mature capsule.—e. Branch, showing decurrent leaf base.—f. Cross section of stem.

mersed, slightly to distinctly winged, the wings up to 1.8 mm broad. Stolons several from lower nodes, often seen in the flowering season, 8–65(–95) cm long, 0.7–2.5 mm diam., the leaves often purplish, especially on the abaxial surface, variable in shape, ranging from orbicular, rotund, oblanceolate to (broadly) elliptic, 4–26 mm long, 4–15 mm wide, base attenuate into petioles 1.5–10 mm long. Cauline leaves lance-elliptic, very narrowly elliptic to linear (those of lower stems sometimes oblanceolate or oblance-elliptic), 18–100 mm long, 2–12.5 (–20) mm wide, those on the branches that subtend

flowers often 2–4 times smaller than those on the main stem, the apex acute to narrowly acute, margin with remote but pronounced hydathodal glands, very occasionally minutely papillose-serrulate on the upper margin, base narrowly cuneate or narrowly acute, sessile or with petioles up to 3 mm long. Stipules dark brownish purple, triangular-ovate or lanceolate, succulent, 0.2–0.4 mm long, 0.1–0.3 mm wide. Flowers in upper leaf axils, sometimes rather congested and in an inflorescencelike arrangement. Sepals creamy white within, the apex pale green, broadly ovate-deltate and boat-shaped, flaring outward, apex acute or acuminate, 2–4 mm long, 1.6–4 mm wide, margin smooth or minutely papillose-serrulate. Petals 0. Anthers 0.55–0.9 mm long; filaments nearly translucent, 1.1–1.7 mm long, slightly dilated toward the base. Pollen grains shed singly. Nectary disc bright yellow, square with rounded corners, raised 0.5–0.8 mm on top of the ovary, 2–3.3 mm across, prominently 4-lobed, glabrous. Style pale green, 0.8–1.3 mm long, glabrous; stigma light yellowish, subglobose, 0.25–0.75 mm across, shallowly 4-lobed on top. Capsules glabrous, obpyramidal, winged on the corners, 3–5 mm long, 2.8–4.5 mm wide (including both wings), the wings ca. 0.5–0.9 mm broad, smooth or minutely papillose, central portion on each side of the wall often somewhat bulging longitudinally, sessile or with pedicels up to 0.8 mm long. Bracteoles flanking capsule base, lance-elliptic or narrowly so, 2.4–4.7 mm long, 0.6–1.5 mm wide, glabrous, margins minutely papillose or smooth. Seeds light brown, ellipsoid, slightly curved on both ends, 0.6–0.7 mm long, 0.3–0.35 mm wide, the surface cells elongate transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 24$.

Distribution. The habitats of *L. alata* include ditches; shores of ponds and lagoons; peaty or sandy swales; open cypress swamps; sandy borrow pits in open pine woods; swampy, flat outcrops of oolitic rocks; wet savannas; tidal flats; brackish marshes; sandy beach strands; and hammocks. This species occurs along the eastern Coastal Plain from southeastern Virginia through eastern North Carolina, with sporadic populations in eastern South Carolina and Georgia; it reaches its southern limit at localities scattered throughout the Florida peninsula. To the west this species extends along the Gulf Coast through the Florida panhandle into southern Alabama, Mississippi, and extreme eastern Louisiana (Fig. 38). Proctor (1982) reported disjunct populations from Jamaica. Flowering from June to October; fruiting from July to November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., ca. 7 mi. W of Gulf Floors, *Kral 32612* (MO, SMU, VDB). FLORIDA: Bay Co., ca. 10 mi. W-NW of Mexico, *Kral 22985* (VDB). Brevard Co., SW shore of Lake Poinsett, 0.5 mi. N of St. Johns River inlet, *Kral 5335* (DS, FSU, NCU, NO, SMU). Broward Co., near E gate of Alligator Alley, *Lakela & Meaghen 31895* (NCU, NY, USF). Citrus Co., Chassahowitzka, *Genelle & Fleming 1551* (GA, USF). Collier Co., 4.8 mi. W of Monroe Station on N side of US Hwy. 41, *Peng et al. 4242* (MO). Dade Co., 2.5 mi. W of Pinelands, on main road of Everglades National Park, between Pinelands and Pa-Hay-Okee Overlook, *Peng et al. 4205* (MO). Dixie Co., 3 mi. SE of Hines, *Kral & Redfearn 3040* (FSU, NY, USF). Duval Co., near Jacksonville, *Curtiss 929* (C, F, FI, FLAS, GA, GH, MO, MSU, NY, P, US). Escambia Co., inland from Gulf Beach, SW Pensacola, *Kral 17602* (VDB). Franklin Co., 38.8 mi. W of jct. (one that is closer to St. Teresa Beach) of US Hwys. 98 & 319, *Peng et al. 4344* (MO). Gulf Co., 2 mi. E of Mexico Beach, *Godfrey & Henderson 62980* (FSU, LL). Hendry Co., *Atwater M-74* (FLAS). Hernando Co., Weekiwachee River, below the Springs, *Godfrey & Hawk 63101* (FSU). Hillsborough Co., Tampa, 1876, *Garber s.n.* (F, US). Lee Co., Myers, *Hitchcock 113* (F, GH, MO, NY, US). Levy Co., near Yankeetown, *Cooley et al. 6971* (FSU, NCU, USF, VDB). Manatee Co., north fork of Manatee River, S of State Rd. 62 and SW of Duette, *Shuey 1768* (USF). Marion Co., Rainbow River, between Dunellon and Rainbow Springs, *Godfrey 63112* (FSU, MO). Martin Co., jct. of Hwy. C-708 and FL Hwy. 76, on S side of ditch on Hwy C-708, *Peng et al. 4203* (MO). Monroe Co., ca. 8 mi. N-NW of Card Sound from Florida City of Key Largo, *Ferborgh & Brockman 287* (FSU). Okaloosa Co., Santa Rosa Island, W of Destin, *McDaniel 4978* (FSU). Orange Co., Killarney, 1889, *Veslulund s.n.* (S). Palm Beach Co., SW of headquarters of Loxahatchee National Wildlife Refuge, ca. 10 mi. W of Gulf Stream, 1970, *Poltevint s.n.* (FLAS). Pinellas Co., Clearwater, *Rolfs 592* (F). Polk Co., near N end of Lake Pierce, 1963, *Conard s.n.* (FLAS). Putnam Co., 0.5 mi. N of Welaka, 1940, *Laessle s.n.* (FLAS). Santa Rosa Co., Blackwater River, vicinity of Milton, *Godfrey 75471* (FSU). Seminole Co., 2 mi. E of Geneva, *Kral 5091A* (FSU, SMU). Taylor Co., ca. 20 mi. NW of Cross City, *Godfrey & Houk 60297* (DUKE, FSU, LL, MSU, NCU, SMU). Volusia Co., 4 mi. S of jct. FL Hwys. 44 and 415, *Kral 18436* (VDB). Wakulla Co., St. Marks Wildlife Refuge, *Godfrey 55760* (FLAS, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF). GEORGIA: Camden Co., White Oak River, 1902, *Harper s.n.* (F, GH, MO, NY, US). LOUISIANA: St. Tammany Parish, ca. 2.25 mi. S of LA Hwy. 90, between West Pearl River and Mill Bayou, *Darwin & Sundell 676* (NO). MISSISSIPPI: Hancock Co., S of Kiln off MS Hwy. 45, *Rogers 1595* (NCU). Harrison Co., Ship Island, *Tracy & Lloyd 230* (E, F, GH, MO, MSC, NY, US). Jackson Co., Horn Island, *Godfrey & Channel 53720* (DUKE, FSU, GH, NY). NORTH CAROLINA: Brunswick Co., Long Beach, *Godfrey 48436* (FSU). Camden Co., E side of Pasquotank River on US Hwy. 158, E of Elizabeth City, *Bozeman & Radford 11531* (C, CM, FLAS, NO, SMU, TENN, TEX, U, UNA, USCH, WCUH, East Carolina Univ. herbarium). Carteret Co., SE of Mullet Pond on Shackleford Banks, *Anderson 408* (DUKE, SMU). Craven Co., New Bern, *Kearney 1961* (US). Currituck Co., Northwest River, near Moyock, *Blomquist 14379* (DUKE). Dare Co., 6 mi. S of Buxton, *Radford et al.*

7593 (GH, NCU). Gates Co., near Sunbury, s.d., *Le Conte s.n.* (NY). Hyde Co., Ocracoke Island, *Kearney 2325* (US). New Hanover Co., Wrightsville Sound, 1963, *Ahles & McCrary s.n.* (NCU). Onslow Co., Bear Island or Hammock Beach State Park, W quarter of island, *Wilbur 9576* (DUKE). SOUTH CAROLINA: Charleston Co., Santee River, N of McClellanville, *Godfrey & Tryon 718* (GH). Horry Co., Myrtle Beach, 70th Ave. N & US Hwy. 17, *Raven 18719* (DS, NCU). Jasper Co., 0.4 mi. SW of Neue River on SC Hwy. 170, *Ahles & Bell 18134* (NCU). VIRGINIA: Norfolk Co., Northwest River below Northwest, *Fernald & Long 14965* (C, GH, S). Princess Anne Co., along Blackwater River, SW of Pungo Ferry, *Fernald & Long 13981* (GA, GH, MO, NY, SMU, TENN, TEX, US). JAMAICA: Hanover Co., in the Great Morass, ca. 1.9 mi. SW of Logwood, *Proctor 37134* (FTG, GH, IJ, MO). Westmoreland Co., ca. 2.7 mi. N-NE of Negril, inland from milepost 23, *Proctor 37733* (F, FTG, IJ).

Ludwigia alata has been confused with *L. lanceolata* (Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982; Clewell, 1985), owing to their similarity in being glabrous, apetalous, and most notably, in having winged, obpyramidal fruits, a character not shared by other species of sect. *Microcarpium*. Raven & Tai (1979) reported the chromosome numbers of *L. alata*. They reported tetraploid counts of $n = 16$ and hexaploid counts of $n = 24$ as a result of not differentiating *L. lanceolata* from *L. alata*. It has now become clear that *L. alata* is a hexaploid and *L. lanceolata* is a tetraploid (Peng, 1988). In my biosystematic study (1988), I reported that reciprocal artificial hybrids between the two species exhibit a modal meiotic configuration of 16 bivalents and 8 univalents, which suggests that they have two genomes in common. Similar results were obtained when the hexaploid *L. alata* was crossed with any of the other tetraploid species of sect. *Microcarpium*. Cytogenetic and morphological data suggest that *L. alata* may have originated following hybridization between the tetraploid *L. lanceolata* and the diploid *L. microcarpa* or populations ancestral to them (Peng, 1988).

Despite their superficial resemblance, *Ludwigia alata* differs sharply from *L. lanceolata* in that the pollen grains are shed singly in *L. alata* and as tetrads in *L. lanceolata* (Praglowski et al., 1983), and the seed surface cells are columnar in *L. alata* vs. suborbicular in *L. lanceolata*. Other characters used by monographers to differentiate the two species include seed shape (ovoid in *L. alata* vs. cylindric in *L. lanceolata*) and sepal shape and size (slightly longer in length than width and nearly as long as the capsule in *L. alata* vs. about as long as wide, shorter than the capsule in *L. lanceolata*) (Small, 1933; Munz, 1944, 1965). These characters, however, are not always clear and reliable.

The leaf base is usually decurrent in *Ludwigia alata*, resulting in the winged stem. The wings are up to 1.8 mm wide in extreme cases. In *L. lanceolata*, by contrast, the stems are nearly smooth. However, the character of the winged stem in *L. alata* is too variable to be diagnostic.

Ludwigia alata has, like all other tetraploids of the section, lost its petals in the course of evolution. In a specimen collected from Duval Co., Florida (*Creager 639*, NCU), one vestigial petal is present on a single flower. Progeny of *Peng 4205* collected from Dade Co., Florida, exhibited minute, vestigial petals on some flowers, too, in greenhouse cultivation. Although normally lacking petals, *L. alata* has whitish sepals that flare outward. This character, along with the fact that the distance between the androecium and the gynoecium is such that mechanical self-pollination cannot usually occur, indicates that *L. alata* is an obligate cross-pollinator. By contrast, *L. lanceolata* has greenish, ascending sepals and is modally self-pollinating. *Ludwigia alata* and *L. lanceolata* are compared in Table 5.

Ludwigia alata occurs with *L. curtissii*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. simpsonii*, and *L. suffruticosa*. Natural hybrids between *L. alata* and *L. pilosa*, and between *L. alata* and *L. suffruticosa*, all of which require insect vectors to effect pollination, are abundant. (See Peng [1988] for voucher information of such natural hybrids.) The hybridity of field populations of *L. alata* × *L. pilosa* is initially suggested by the combination of the winged ovaries/capsules and minute, uniform pubescence found in these plants. Of the 15 taxa in sect. *Microcarpium*, only *L. alata* and *L. lanceolata* have winged capsules, and they are glabrous. *Ludwigia pilosa* and *L. ravenii* are consistently pubescent, and *L. sphaerocarpa* is variable in vestiture; none of them has winged capsules. The parentage of the hybrids between *L. alata* ($n = 24$) and *L. pilosa* ($n = 16$) is further verified by (1) their reduced level of stainable pollen (ca. 45–70%, which is indicative of a heteroploid cross), and (2) a mixture of columnar and isodiametric cells and some other irregular cells on their seed surface (among the pubescent putative parental species, only *L. pilosa* differs significantly in the seed surface pattern from *L. alata*).

Natural hybrids between *Ludwigia suffruticosa* ($n = 16$) and *L. alata* ($n = 24$) are difficult to recognize in the field. They are very similar to *L. alata* in general aspect, having winged capsules and slightly winged stems, as well as pollen grains shed singly. However, they differ from *L. alata* in that their stems are less branched; their flowers are borne only in the upper leaf axils of each

branch; their capsules are smaller, presumably as a result of reduced seed set; and their seed surface consists of a mixture of many columnar but relatively shorter cells, as well as somewhat isodiametric cells (typical of *L. suffruticosa*), and is irregular.

9. Ludwigia sphaerocarpa Elliott, Sketch Bot. S. C. & Ga. 1: 213. 1817. *Isnardia sphaerocarpa* (Elliott) DC., Prodr. 3: 61. 1828. *Ludwigia sphaerocarpa* Elliott var. *typica* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. South Carolina: Orangeburg Co., in swampy grounds near Orangeburg, flowers in August, s.d., *S. Elliott s.n.* (holotype, CHARL; photographs, GH, MO; possible isotype, PH). Figure 51.

Ludwigia sphaerocarpa Elliott var. *deamii* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Indiana: Porter Co., low border of Lake Walker, NW of Baileytown, 23 Aug., 1925, *C. C. Deam 42350* (holotype, GH).

Ludwigia sphaerocarpa Elliott var. *jungens* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Virginia: Princess Anne Co., Cape Henry, pool in sandy barrens, 23 Sep., 1933, *M. L. Fernald & L. Griscom 2862* (holotype, GH).

Ludwigia sphaerocarpa Eliott var. *macrocarpa* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Massachusetts: Plymouth Co., Lakeville, stony shore of Quitacas Pond, 27 Aug., 1899, *W. P. Rich s.n.* (holotype, GH).

Stems erect, well-branched, (40–)60–110 cm tall, glabrous to densely strigillose; aerenchyma often very prominent in the lower part. Stolons many, up to 90 cm long, 2–3.5 mm thick, floating, sometimes branched, the leaves purplish, narrowly elliptic or oblanceolate, sometimes spatulate, 9–30 mm long, 4–8(–13) mm wide, glabrous to densely strigillose, apex acute or obtuse, margin with distinct hydathodal teeth or sometimes subentire, base attenuate into ± winged petiole 1.5–3 mm long. Cauline leaves narrowly elliptic or lanceolate to sublinear or linear, those on the main stem (26–)60–100 mm long, 4.5–11(–16) mm wide, those of the branch 20–50(–60) mm long, 2.5–5(–6) mm wide, glabrous to densely strigillose, apex acute to very narrowly acute, margin entire, hydathodal glands often visible in main cauline leaves, base attenuate or narrowly cuneate into petioles 1–4(–10) mm long. Stipules reddish purple, lanceolate or deltoid, 0.15–0.4 mm long, 0.1–0.2 mm wide. Flowers in upper leaf axils, lax to very crowded on branches. Sepals green without, yellow within, ovate-deltoid, ascending, 2–3.5(–4) mm long, 1.6–3(–3.3) mm wide, glabrous to densely strigillose on both surfaces, apex acuminate, margin entire. Petals 0. Anthers 0.5–0.8 mm long, filaments yellow, 1–1.7 mm long, slightly dilated toward base. Pollen grains shed as tetrads. Nectary disc bright yellow, raised 0.4–0.6 mm on ovary apex, 1.5–3 mm across, 4-lobed, glabrous to short hirtellous between the lobes. Style yellow, 0.55–1(–1.25) mm long, glabrous to strigillose, especially below. Stigma yellow, subglobose, 0.35–0.5 mm long, 0.4–0.7 mm thick. Capsules sometimes pinkish, subglobose, (1.8–)2–4(–4.5) mm long, 2–4 mm thick, glabrous to densely strigillose, pedicels 0.5–1.2(–2.3) mm long. Bracteoles subopposite on short pedicel, rarely flanking capsule base, linear to very narrowly lanceolate, rarely lanceolate, 0.5–1.5 mm long. Seeds brown to light brown, elliptic, 0.45–0.7 mm long, 0.25–0.35 mm wide, the surface of a mixture of columnar cells, these elongate and transversely elongate to the seed length, sometimes oblique, the orientation of cells often variable from seed to seed. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. sphaerocarpa* grow in drainage ditches, on stream or pond shores, and in river marshes, swales, swamp forests, edges of limestone sinks, peaty bogs in pastures, and interdunal marshes. This species has an extensive distribution along the Atlantic coast, ranging from Massachusetts to northcentral Florida. To the west it extends through the panhandle of Florida, southwestern Georgia, southeastern Alabama, central and southwestern Louisiana, and reaches eastern Texas. Disjunct populations occur in southcentral Tennessee, extreme southwestern Indiana, along Lake Michigan in northeastern Illinois and northwestern Indiana, and in westcentral New York (Fig. 52). Flowering from June to September; fruiting from August to November.

Representative specimens examined. U.S.A. ALABAMA: Covington Co., Blue Pond, Conecuh National Forest, SW of Andalusia, *Kral 44739* (ENCB, GA, GH, MO, SMU, US, VDB). Elmore Co., ca. 5.5 mi. E-SE of jct. with US Hwy. 231 & Co. Rd. 4, *Wiersema 325* (UNA). Geneva Co., 1 mi. SW of Hartford, *McDaniel 7654*. CONNECTICUT: Middlesex Co., Killingworth, *Eames 11046* (GH). New London Co., Groton, *Enequist 299* (NY). New Haven Co., N Guilford, 1906, *Bartlett s.n.* (GH). DELAWARE: Kent Co., Felton, 1873, *Canby s.n.* (F). New Castle Co., Townsend, 1862, *Canby s.n.* (NCU). Sussex Co., Ellendale, *Commons s.n.* 1892 (GH, NY). FLORIDA: Dixie Co., 4 mi. N of Suwannee, *Godfrey 56178* (FSU, GA, GH, NY, TENN, USF). Flagler Co., near Korona, 1944, *Butts s.n.* (GH). Franklin Co., 0.5 mi S of the mouth of the Ochlockonee River, *Godfrey 54110* (FSU, GH, NY). Gilchrist Co., 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Holmes Co., just E of Westville, *Godfrey 59013* (FSU, in 2 sheets). Jackson Co., Lake Seminole, Wildlife Refuge Area, *Monoson 55* (GH). Jefferson Co., ca. 4 mi. E of Wacissa, *Godfrey 63173* (FSU). Leon

FIGURE 51. *Ludwigia sphaerocarpa.* All but a′ from South Carolina (Jasper Co., *Peng et al. 3986*, MO); a′ from South Carolina (Jasper Co., *Boufford et al. 21650*, MO).—a. Habit, erect stem.—a′. Basal stolon.—b. Flower.—c, c′. Adaxial and abaxial views of stamen.—d. Fruit.—e. Cross section of fruit.

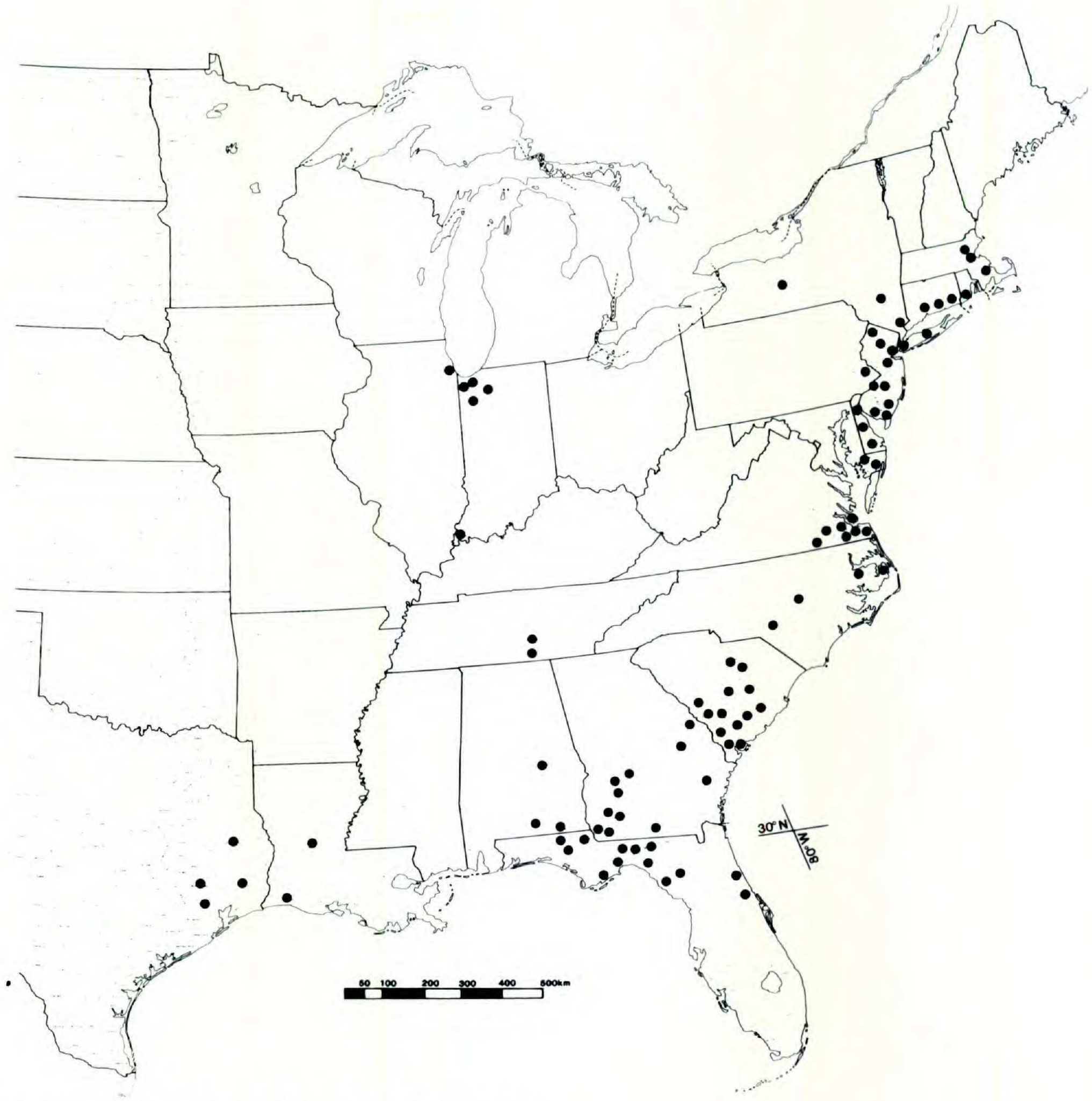

FIGURE 52. Distribution of *Ludwigia sphaerocarpa*.

Co., 2 mi. SE of Tallahassee, *McDaniel 3708* (FSU). Madison Co., 6 mi. E of Greenville, *Wiegand & Manning 2199* (GH). St. Johns Co., 1.9 mi. N of jct. of FL 207 and C-305, on FL 207, *Peng et al. 4159* (MO). Taylor Co., 1.2 mi. SE of Salem, *Godfrey 64726* (DS, LL, NCU). Volusia Co., 2 mi. N of Barberville, 1943, *West & Arnold s.n.* (FLAS). Wakulla Co., 6 mi. E of Sopchoppy along Ochlockonee River, *Morar 28* (DUKE, FLAS, FSU, MSC, US). Washington Co., *Curtiss 925* (C, F, GH, NCU, NY, S, UPS, US). GEORGIA: Baker Co., SW corner, *Duncan 4055* (GA). Burke Co., near Shell Bluff, *Eyles 6478* (GA). Decatur Co., along Hwy. 97, 1.3 mi. S-SW of Faceville, *Thorne & Davidson 17147* (FSU, GA). Dooly Co., 2 mi. N of Pinehurst, *Kral 51611* (VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on US 1, on Ohoopee River, *Peng et al. 4026* (MO). Lee Co., W of Leesburg by GA Hwy. 32, *Kral 56334* (VDB). Long Co., 1.5 mi. SW of jct. of US 301 and 25, and GA 99, on US 301 and 25 near Altamaha River, *Peng et al. 4115* (MO). Lowndes Co., near Valdosta, *Curtiss 6710* (GA, GH, MO, NY). Mitchell Co., 5 mi. N of Camilla, *Thorne 5792* (GA). Seminole Co., Ray's Lake, lots 99 and 102, Dist. 21, *Thorne & Davidson 16764* (FLAS). Sumter Co., *Harper 553* (F, GH, MO, NY, US). ILLINOIS: Cook Co., Chicago, 1860, *Scammon s.n.* (F). INDIANA: Jasper Co., ca. 1.8 mi. S of Co. Rd. 10 and 0.8 mi. W of Co. line, *Friesner 22974* (FLAS, LL, S, SMU). Lake Co., Pine, 1896, *Unbach s.n.* (DS, F, MSC, NY, S, US). Porter Co., Wilson (Dune Park), 1958, *Bennett s.n.* (F, NY, SMU, W). Posey Co., Scuffle Pond in the Nolta Erwin Woods, ca. 8 mi. SW of Mt. Vernon, *Deam 59451* (NY). Starke Co., SW corner of Bass Lake, *Friesner 16306* (GH, MO, SMU). LOUISIANA: Cameron Parish, Lacassine Wildlife Refuge, *Thieret 16410* (DUKE, GA, MO, SMU). Rapides Parish, Red River, 1840, *Hale s.n.* (US). MARYLAND: Wicomico Co., Salisbury, 1889, *Canby s.n.* (NY). Worcester Co., 15 mi. N of Berlin, *O'Neill 7489* (CAS, DS, F, ND, NY). MASSACHUSETTS: Middlesex Co., Concord River, Bedford, 1908, *Fernald s.n.* (GH). Plymouth Co., Middleboro Ponds, Lakeville, *Churchill 595* (MO). Suffolk Co., near Boston, 1830, *Greene s.n.* (NY). NEW JERSEY: Atlantic Co., Hammonton, *Gershay 505* (GH). Burlington Co., Atsion, *Fogg 4697* (GH, TENN). Cape May Co., Bennett, 1913, *Stone s.n.* (NY). Cumberland Co., 1902, *Holmes s.n.* (FLAS, GA). Gloucester Co., Nortonville, *Lippincott 42* (GH). Middlesex Co., Spotswood, *Taylor 2586* (NY). Morris Co., Denmark Pond, *Mackenzie 4758* (MO, NY, S). Sussex Co., Hopkins Corners, 3 mi. NE of Lafayette,

1935, *Edwards s.n.* (NY). NEW YORK: Queens Co., N of Jamaica, Long Island, 1900, *Bicknell s.n.* (NY). Richmond Co., Staten Island, 1879, *Briton s.n.* (GH). Suffolk Co., Long Island, Long Pond, Sag Harbor, *Muenscher & Curtiss 6357* (GH, NY, US). Ulster Co., Esopus Pond, *Muenscher & Curtis 5779* (GH). Westchester Co., Lake Mohegan, 1887, *Martens s.n.* (C, DUKE, F, GH, NY, US). Yates Co., s.d., *Sartwell s.n.* (US). NORTH CAROLINA: Dare Co., along Hwy. 345, 3.75 mi. N of Wanchess, Roanoke Island, *Radford & Stewart 895* (NCU). Hoke Co., 4 mi. SW of Ashley Heights, *Ahles 36372* (NCU). Johnston Co., 5 mi. S-SW of Princeton, *Radford 27780* (CM, GH, FLAS, NCU, NY, SMU, TENN, VDB). Washington Co., 3.6 mi. S of Cherry, *Radford 38909* (NCU). PENNSYLVANIA: Bucks Co., Bristol, 1864, *Porter s.n.* (P). Westmoreland Co., 1878, *Pierron s.n.* (JE). RHODE ISLAND: Washington Co., Worden's Pond, South Kingstown, 1931, *Collins s.n.* (GH). SOUTH CAROLINA: Aiken Co., 1.4 mi. E of Monetta on SC Hwy. 39 and 0.2 mi. N on SC Hwy. 266 (near Williams Cemetery), *Massey & Massey 2995* (MO, NCU). Bamberg Co., 4 mi. SW of Denmark on Co. Rd. 26, *Ahles 37601* (NCU). Barnwell Co., Savannah River Operations Area of the Atomic Energy Comm., 1964, *Kelley s.n.* (USCH). Berkeley Co., 10.3 mi. W of Pineville on SC Hwy. 45, *Ahles & Baird 54901* (NCU). Calhoun Co., Riley, along US Hwy. 601, *Ahles 35324* (NCU). Clarendon Co., 13 mi. SW of Manning, *Godfrey & Tryon 1457* (DUKE, F, GH, MO, NY, US). Colleton Co., 4.2 mi. E of Smoaks on SC Hwy. 217, *Ahles & Bell 17889* (NCU). Dorchester Co., along US Hwy. 15, N of SC Interstate 15, *Leonard & Radford 1988* (NCU). Hampton Co., 2.1 mi. S of Gifford on US Hwy. 321, *Bell 3948* (NCU, USF). Jasper Co., 6.6 mi. N of SC Hwy. 46 on US Hwy. 17, N of Hardeeville, *Peng et al. 3986* (MO). Kershaw Co., Adams Millpond, 2.5 mi. NE of US Hwy. 1 at Camden, on SC Hwy. 15, *Radford et al. 11388* (B, BOON, DS, East Carolina Univ. Herb., MEX, MISS, NCU, S, TEX, UNA, WCUH). Lee Co., McGurts Creek, near US Hwy. 15 at Mechanicsville, *Radford 27252* (FSU, NCU). TENNESSEE: Coffee Co., Goose Pond on AEDC land along access hwy., 1973, *DeSelm et al. s.n.* (TENN). Franklin Co., ca. 8 mi. W of Winchester, 1976, *Kral s.n.* (VDB). VIRGINIA: Greensville Co., *Cephalanthus* swamp, ca. 1 mi. N of Skipper's, *Fernald & Long 8788* (GH). Isle of Wight Co., Cat Pond, S of Berns Church, *Fernald & Long 7547* (GH, MO). Nansemond Co., ca. 7 mi. E-NE of Suffolk, *Kral 13766* (FSU, VDB). Norfork Co., Lake Drummond, Great Dismal Swamp, W of Wallaceton, *Fernald & Long 13402* (GH, MO, NY, SMU, TENN, US). Princess Anne Co., E of T-1, N of RR, near picnic shelter, *Egler 40281* (NY). Sussex Co., N of Stony Creek, *Fernald & Long 8790* (GH). York Co., NW of Grafton, *Fernald & Long 7548* (GH, NY, US).

Ludwigia sphaerocarpa is highly polymorphic. Its variability is largely the result of its wide geographic (and latitudinal) range, the sporadic, semi-isolated distribution of the populations, the interaction of differential adaptation and genetic drift made possible by its pattern of distribution, and its possible hybrid nature (see below). Hybridization with *L. pilosa* in regions where their ranges overlap apparently provides an important source of variability in *L. sphaerocarpa*.

Populations of this species consist of individuals that vary in overall pubescence, leaf shape and size, fruit size, and density of fruits on branches. Fernald & Griscom (1935) recognized var. *jungens*, var. *macrocarpa*, and var. *deamii* based on various combinations of these characters. In their treatment, the varieties were separated as follows:

Rameal leaves strongly reduced, glabrous or pubescent, lanceolate.
  Mature hypanthium small, 2.5–3.2 mm long, 2.8–4 mm broad, averaging broader than long.
    Hypanthium pubescent; leaves narrowly linear-lanceolate and attenuate ..... var. "*typica*" [var. *sphaerocarpa*]
    Hypanthium, branches, and leaves pubescent; leaves more broadly lanceolate, not attenuate ..... var. *jungens*
  Mature hypanthium larger, 3.5–4.6 mm long, 3.2–4 mm broad, averaging longer than broad ..... var. *macrocarpa*
Rameal leaves scarcely smaller than the primary ones, pubescent, narrowly oblong; stems pubescent; hypanthium pubescent, 3 mm long, about as wide ..... var. *deamii*

In his revisions of the New World species of *Ludwigia*, Munz (1944, 1965) reduced var. *deamii* to synonymy under var. *jungens* and presented the following key to the varieties:

Fruit crowded on branches, 3.5–4.5 mm long, not as wide. Massachusetts to New Jersey ..... var. *macrocarpa*
Fruit not crowded on branches, 2–3.2 mm long, usually wider.
  Main stems and leaves usually glabrous; principal leaves linear-lanceolate and over 7 cm long. Rhode Island to Florida ..... var. *sphaerocarpa*
  Main stems and leaves pubescent to strigose, lanceolate, usually less than 7 cm long. New Jersey to North Carolina, Michigan, and Indiana ..... var. *jungens*

A study of numerous herbarium specimens not available to Fernald & Griscom (1935) and Munz (1944, 1965) has revealed that correlations between these characters are not consistent; they often intergrade. Indeed Munz (1944) noted that "var. *typica* (the typical variety) and var. *jungens* intergrade freely." Under *Ludwigia sphaerocarpa* var. *macrocarpa*, he also wrote, "New Jersey material is sometimes difficult to distinguish from var. *typica* (the typical variety)." In my opinion, it is best to treat *L. sphaerocarpa* as representing an assemblage of variable populations without recognizing the infraspecific taxa. These populations share the following diagnostic characters: subglobose capsules, diminutive bracteoles (shorter than 1.5 mm long), and ovate-deltoid, yellowish, conspicuous sepals.

It is also of interest to note that, although the seed surface cell pattern is generally very regular within populations of members of *Ludwigia* sect. *Microcarpium* (Figs. 19–28, 30–34), this is not the case for *L. sphaerocarpa* (Fig. 29). The seed surface is arranged in columnar cells both transversely elongate and parallel to the seed length, the former alignment often predominating in the central part of the seeds. Seeds with variously oriented surface cells are also seen in some populations. Comparison of the seed surface pattern in populations of *L. sphaerocarpa* with that of various artificial hybrids strongly suggests that earlier hybridizations within the interfertile tetraploid group of sect. *Microcarpium* may have resulted in this widespread series of populations that are more or less stabilized in some of their characteristics, and such hybridizations may still be contributing to the variability of this series of populations.

The biosystematic study of *Ludwigia* sect. *Microcarpium* (Peng, 1988) demonstrated that hybrids between species that differ in their seed surface cell pattern always show a mixture of cell types or cells of intermediate shapes and sometimes of randomly oriented cells. Similarly, hybrids resulting from crossing a densely hirtellous species with a glabrous one always exhibit minutely villous or strigillose pubescence. Of the tetraploid *Ludwigia* taxa that are interfertile with *L. sphaerocarpa*, *L. ravenii* and *L. glandulosa* subsp. *brachycarpa* are the only ones with columnar seed surface cells elongate transversely to the seed length, whereas *L. polycarpa* and *L. glandulosa* subsp. *glandulosa* are the only taxa with columnar seed surface cells elongate parallel to the seed length. Both subspecies of *L. glandulosa*, having narrow, subcylindrical capsules, are unlikely to be parents of *L. sphaerocarpa*. In seed surface pattern and overall pubescence, *L. ravenii* (densely hirtellous) and *L. polycarpa* (glabrous) seem to be suitable parental candidates. However, that they both have oblong-obovoid capsules and are highly autogamous, in contrast to subglobose capsules and outcrossing habit of *L. sphaerocarpa*, renders it unlikely that they have been involved directly in the formation of *L. sphaerocarpa*. One or possibly both parents of *L. sphaerocarpa* are likely extinct.

The morphological variation in *Ludwigia sphaerocarpa* is further complicated by its frequent natural hybridization with *L. pilosa*, which has apparently resulted in many hybrid swarms or introgressed populations. These plants generally exhibit varying degrees of intermediacy in diagnostic characters such as seed surface pattern, overall pubescence, bracteole size, sepal shape and size, and leaf shape. The following specimens show intermediacy in at least two of the above characters or a combination of some of the diagnostic features of *L. pilosa* with some of those of *L. sphaerocarpa*:

U.S.A. ALABAMA: Escambia Co., 2.5 mi. N of Atmore Prison, off Hwy. 21, *Harvey 275* (UNA). FLORIDA: Citrus Co., 5 mi. S of Homosassa, *Kral 7772* (FLAS, GH, NCU, US, USF, VDB). Columbia Co., 2.5 mi. N of Ellisville, along U.S. Hwy. 41, *Raven 18634* (DS). Dade Co., near Lake Okeechobee, *Fredholm 6182* (GH, NY, US). Duval Co., near Jacksonville, *Curtiss 4324* (DS, ND, NY, US), *Curtiss 5214* (GH). Highlands Co., S end of Lake Istokpoga, *Raven 18683* (DS, NCU); E of Sebring, Carter Creek Swamp, 1948, *Garrett s.n.* (FLAS); 2 mi. S of Parker Islands, *Brass 15325* (US). Hillsborough Co., River State Park, along U.S. Hwy. 301, 1978, *Rochow & Lopez s.n.* (USF); 1 mi. N of bridge on Tarpon Springs–Lake Fern Road, *Poppleton 699* (DS). Lake Co., in the vicinity of Eustis, *Nash 1041* (F, GH, MO, MSC, NY, PH, S, US). Madison Co., 6.8 mi. W of Greenville, along U.S. Hwy. 90, *Raven 18629* (DS); 10 mi. S of Greenville, *Kral 3769a* (FSU, GA, GH, NY, SMU, TENN, UNA, USF). Manatee Co., NE of intersection of state roads 62 & 39, *Shuey 1712* (USF). Polk Co., ca. 3.3 mi. SW of Polk City, along FL Hwy. 33, *Smith & Myint 586* (FLAS, FSU, NCU). St. Johns Co., St. Augustine, 1875, *Reynolds s.n.* (F, FLAS, MO, NY—2 sheets, PH); 1876, *Garber s.n.* (FLAS). Wakulla Co., vicinity of Panacea, *Godfrey 60276* (FSU). GEORGIA: Colquitt Co., 8 mi. NE of Moultrie, *Kral 15008* (VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on U.S. Hwy. 1, *Peng et al. 4025* (MO), *Peng et al. 4026a* (MO). Richmond Co., Augusta, Sanitary Dairy Pond, 1924, *Hildebrand s.n.* (DUKE). Wilcox Co., 10.9 mi. NNW of Abbeville, *Hardin & Dunkan 14246* (GA). NORTH CAROLINA: Robeson Co., ca. 1.5 mi. S of Luberton, *Kral 19030* (VDB, mixed with *L. pilosa*). SOUTH CAROLINA: Aiken Co., 1869, *s.c., s.n.* (US); Beaufort Co., St. Helena Island, 1884, *Cuthbert s.n.* (FLAS). Colleton Co., 4.2 mi. E of Smoaks, *Raven 18718* (DS, 2 sheets, NCU). TEXAS: Freestone Co., 5 mi. SE of Dew, on Hwy. 75, *Correll 35249* (LL); 15 mi. SE of Fairfield, *Kral 111* (FSU). Gonzales Co., Ottine, 1936, *Tharp s.n.* (MO, SMU, TEX). Harris Co., Gosby, 1923, *Fischer s.n.* (S, US); Humble, *Tharp 4518* (MO); Sheldon, *Reverchon 2301* (MO). Hardin Co., 1937, *Tharp s.n.* (TEX). Nacogdoches Co., Nacogdoches, *Waller 273* (SMU, TAES). Orange Co., 1.7 mi. N of Mauriceville, *Shinners 25116* (SMU). Wood Co., 2 mi. N of Mineola, *Correll 35021* (LL); Lake Ellis, *Lundell & Lundell 11748* (LL, SMU).

Some of the above putative hybrid populations are from central and southern Florida, where neither typical *Ludwigia pilosa* nor *L. sphaerocarpa* occur (Peng, 1988, fig. 22). This suggests that their physiological characteristics, and thus their ecological tolerances, may differ from those of the parents in such a way as to allow them to occur in novel habitats and areas where neither of their parents can survive.

The following collections are unusual in being densely hirtellous (having erect hairs ca. 0.4–0.8

mm long), but they are otherwise typical of *Ludwigia sphaerocarpa*. They may represent introgressants between *L. sphaerocarpa* and either *L. pilosa* or *L. ravenii*.

U.S.A. FLORIDA: Flagler Co., vicinity of Andalusia, *Godfrey & Reinert 61149a* (FSU). SOUTH CAROLINA: Beaufort Co., 0.8 mi S of Yemassee on Co. Rd. 3, *Bell 4703* (NCU); *Raven 18716* (DS, FLAS, TEX). Hampton Co., 0.8 mi. NNW of Shirley on Co. Rd. 20, *Bell & Ahles 18254* (NCU). Jasper Co., 5 mi. S of Ridgeland, on U.S. Hwy. 17, *Dille & Dille 346* (MO); 7 mi. N of Hardeeville, on U.S. Hwy. 17, *Dille & Dille 349* (MO). TEXAS: Angelina Co., N of Boykin Springs, Angelina National Forest, *Correll 34910* (LL). Hardin Co., between Silsbee and Kountze, S of Hwy. 418, SW of county dump grounds, *Amerson & Watson 228* (LL). Harris Co., Humble, *Tharp 4518* (US). Montgomery Co., 12 mi. W of Cleveland, *Kral 21041* (DS, VDB—2 sheets).

Plants of the following collections were found to have one to three vestigial, yellow petals in some of the flowers:

U.S.A. FLORIDA: Flagler Co., near Korona, 1944, *Butts s.n.* (GH). Wakulla Co., on U.S. 98, 5 mi. W of FL 59, *Dille & Dille 401* (MO). NEW YORK: Suffolk Co., Long Pond, Sag Harbor, *Muenscher & Curtis 6357* (NY).

Judged by their morphology as well as their full seed set, these plants are more likely to be mutants showing an ancestral trait rather than hybrids between *Ludwigia sphaerocarpa* and one of the petaliferous species of sect. *Microcarpium*.

Almost all populations of *Ludwigia sphaerocarpa* are at least sparingly strigillose, especially on the ovary/capsule walls. The following two glabrous collections from Louisiana are exceptional:

U.S.A. LOUISIANA: Cameron Parish, in "The Pool," Lacassine Wildlife Refuge, *Thieret 16410* (DUKE, GA, MO, SMU). Rapides Parish, Red River, 1840, *Hale s.n.* (US).

They seem to parallel the glabrous variants of *Ludwigia linearis* (see above) in which a few glabrous plants may grow intermixed locally with densely strigillose individuals.

Ludwigia sphaerocarpa is one of the few species in sect. *Microcarpium* in which the distance between the androecium and the gynoecium is such that self-pollination is impossible without the intervention of pollen vectors. Although the flowers of *L. sphaerocarpa* are apetalous, their sepals are adaxially yellowish. This, along with the bright yellow nectary disc, which produces copious nectar, attracts many insects to the flowers of this apparently largely outcrossing species.

In the field, *Ludwigia sphaerocarpa* grows with *L. glandulosa*, *L. linearis*, *L. microcarpa*, *L. pilosa*, and *L. polycarpa* and hybridizes with all but the small-flowered, modally selfing *L. microcarpa*. The natural hybrids generally exhibit intermediate morphology, most notably in fruit shape and size, bracteole length, overall pubescence, and seed surface cell pattern. The fruits are plump and contain abundant seeds in homoploid (tetraploid) hybrids. In the heteroploid (triploid) *L. sphaerocarpa* ($n = 16$) × *L. linearis* ($n = 8$), one to four petals were present in most flowers, and seed set was negligible.

In the experimental greenhouse, artificial hybrids have been synthesized between *Ludwigia sphaerocarpa* and the diploid *L. linearis*, *L. microcarpa*, the tetraploid *L. glandulosa*, *L. polycarpa*, *L. suffruticosa*, *L. lanceolata*, *L. pilosa*, the hexaploid *L. alata*, and the octoploid *L. curtissii* (Peng, 1988).

10. Ludwigia pilosa Walter, Fl. Carol. 89. 1788. *Isnardia pilosa* (Walter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. TYPE: U.S.A., "the Carolinas," s.d., *T. Walter 658* (holotype, BM, Walter Herbarium p. 66; photograph, MO). Figure 53.

Ludwigia rudis Walter, Fl. Carol. 89. 1788. TYPE: U.S.A. "the Carolinas," s.d., *T. Walter s.n.* (type not found at BM, Walter Herbarium; possible isotype, P ("No. 3"); photograph, MO).

Ludwigia hirsuta Lam., Encycl. 3: 614. 1792. TYPE: U.S.A. South Carolina: 1785–1792, *J. Fraser s.n.* (holotype, P; photographs, GH, MO).

Ludwigia mollis Michaux, Fl. Bor.-Am. 1: 90. 1803. *Isnardia mollis* (Michaux) Poiret in Lam., Encycl. Suppl. 3: 188. 1813. TYPE: U.S.A. South Carolina: wet places, 1785–1796, *A. Michaux s.n.* (holotype, P; photographs, GH, MO; possible isotype, PH).

Plants hirtellous throughout. Stems much branched, 40–120 cm tall, often with prominent aerenchyma below when submerged in water, the hairs 0.25–0.95 mm long, translucent or spotted with light brown pigments. Stolons up to 2.5 m long, creeping in mud or floating in water, occasionally bearing flowers and fruits, the leaves obovate or elliptic to orbicular, 6.5–20 mm long, 5–11 mm wide, densely hirtellous to nearly glabrous, margin with distinct hydathodal teeth, petioles 2–7 mm long. Cauline leaves (upon drying) usually brownish green adaxially, brown abaxially, elliptic or lance-elliptic to very narrowly so, 15–80(–100) mm long, 3–12(–14) mm wide, those on the main stem usually 1.5–4 times longer than those on the branches, the veins reddish, the hairs 0.3–0.5 mm long, apex acute or narrowly acute, margin entire, hydathodal glands obscure, base acute to narrowly acute or attenuate, sessile or with petioles up to 2(–10) mm long. Stipules brownish purple, ovate to lanceolate, 0.2–0.25 mm long, up to 1 mm

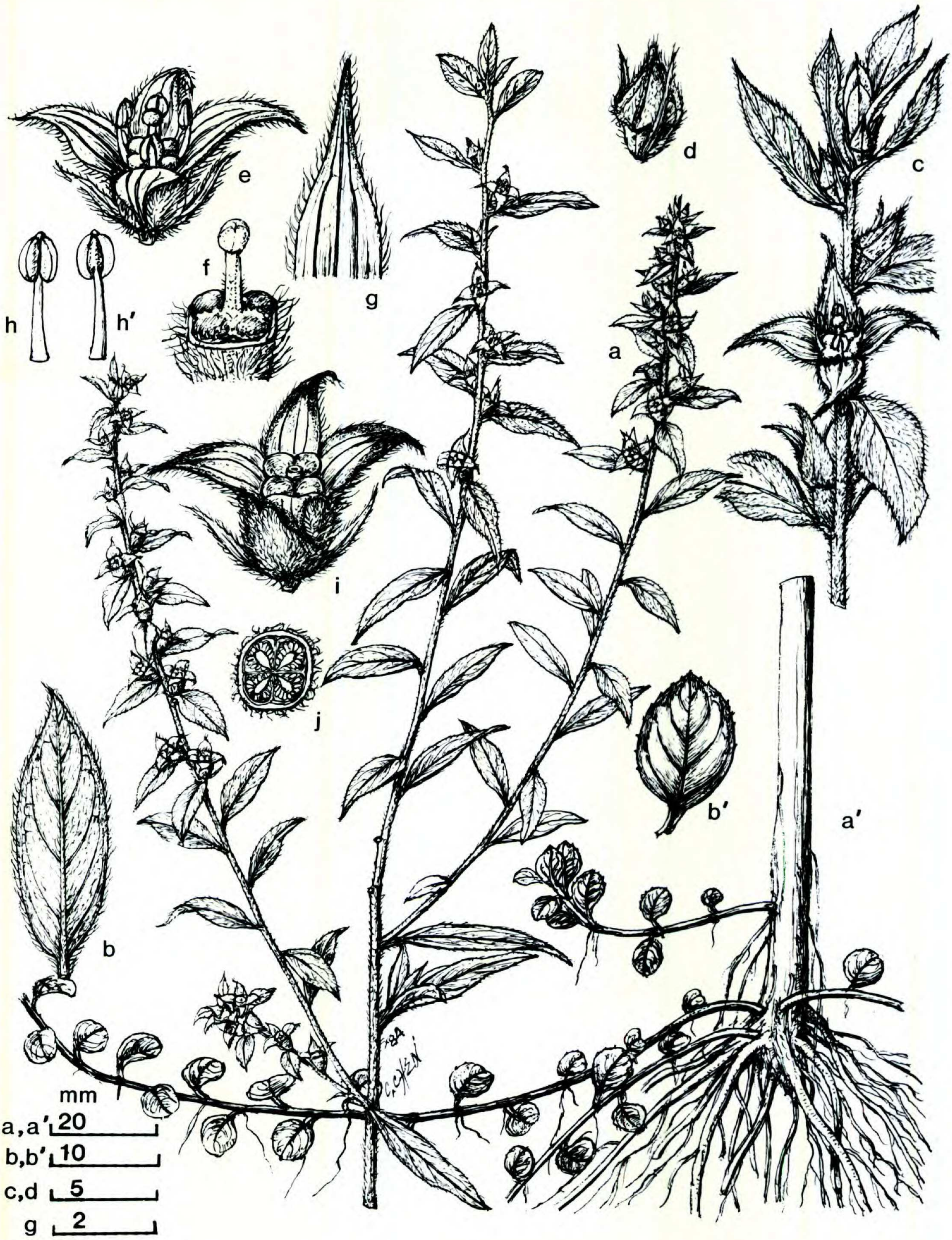

FIGURE 53. *Ludwigia pilosa* (South Carolina: Berkeley Co., *Peng 4397*, MO).—a. Habit, erect stem.—a′. Basal stolons.—b. Cauline leaf.—b′. Stolon leaf.—c. Flowering branch.—d. Flower bud.—e. Flower.—f. Flower, partly dissected to show stigma, style, and disc.—g. Sepal.—h, h′. Adaxial and abaxial views of stamen.—i. Fruit.—j. Cross section of capsule.

wide, usually obscured by hairs on the stem. Flowers usually congested in upper leaf axils. Sepals very conspicuous, creamy white within, usually also tinged with pink along the main veins and edges, occasionally reddish when grown in exposed sites, ovate-triangular or triangular, with 3 parallel main veins that are usually raised and prominent on the adaxial surface, apex elongate acuminate to subcuspidate, ascending with reflexed tips, 3.5–5.5 (–6) mm long, 2–4 mm wide, densely hirtellous within. Petals 0. Anthers 0.6–0.9(–1.3) mm long; filaments yellowish, 1.5–2.5 mm long, distinctly dilated below. Pollen grains shed as tetrads. Nectary disc bright yellow, turning black upon drying, raised 0.3–0.75 mm on top of the ovary, 2–3.8 mm across, indistinctly 4-lobed, densely hirtellous around the style base and often sparsely hirtellous between the lobes. Style 1–2 mm long, sparsely to densely hirtellous, especially below; stigma 0.3–0.6 mm thick. Capsules subglobose or sometimes oblong-obovoid with rounded corners, 3–5 mm long and 3–4.5 mm thick, densely hirtellous, sessile or with pedicels up to 1 mm long. Bracteoles flanking the capsules, attached 1–2.25 mm above capsule base, linear-lanceolate or narrowly elliptic, hirtellous, 3–6.5(–7.2) mm long, 0.25–1.5(–1.7) mm wide. Seeds brown, elliptic oblong or oblong ovoid, slightly curved on both ends, 0.5–0.7 mm long, 0.25–0.35 mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia pilosa* are frequently found in roadside ditches, in river marshes, in swales in sandy pine flats, at edges of pocosins, in peaty bogs, in low grassy savannahs, and in swamp forests. This species is distributed along the Atlantic coast of extreme southeastern Virginia, eastern and central North and South Carolina, southern Georgia, and northern Florida. It extends westward through the Florida panhandle, southern Alabama, Mississippi, and Louisiana, reaching eastern Texas. A disjunct population occurs in northern Alabama (Fig. 54). Flowering from late June through September; fruiting from late July through November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., Fort Morgan Peninsula, *Demaree 35917* (FSU, GH, SMU, USF, VDB). Barbour Co., ca. 5 mi. N of Eufaula on AL I-65, Cowickee Creek camp by Lake Eufaula, *Kral 33185* (VDB). Butler Co., ca. 11 mi. N of Georgiana by AL I-65, *Kral 40892* (VDB). Covington Co., ca. 8 mi. S of Opp, by US Hwy. 331, *Kral 32063* (SMU, VDB). Crenshaw Co., near Dozier, *Reed 2052* (TEX). Dale Co., near Clayhatchee, *Kral 22079* (DS, VDB). Dallas Co., just W of Selma, by Hwy. 22, *Perdue 4155* (FSU, VS). Elmore Co., W side of Elmore, by Mortar Creek, *Kral 40808* (VDB). Escambia Co., 1.3 mi. E of Wawbeek, *Kral 33831* (MO, VDB). Geneva Co., 3.2 mi. S of Hartford on AL Hwy. 167, *Kral 36728* (VDB). Houston Co., just E of jct. S of Spring Hill Church, Cypress Creek Swamp, *Clark 7343* (NCU). Lowndes Co., 10 mi. E of Minter, near Fostoria, *Kral 48927* (VDB). Macon Co., *Earle & Earle 49* (GH, MO, ND-G, NY, US). Madison Co., *Earle & Earle 49* (GH, MO, NY, US). Mobile Co., on Hollinger's Island, *Harper 4087* (GA, MO, NCU, NY, UNA, US, VDB). Pike Co., Spring Hill, *Bush 339* (S). Washington Co., 3.1 mi. S of St. Stevens, *Kral 37234* (FSU, VDB). FLORIDA: Alachua Co., near Waldo, 1936, *Survey s.n.* (FLAS). Bay Co., near Long Beach, *Godfrey & Kral 55075* (FSU, NCU). Bradford Co., near US Hwy. 301, *Radford 8245* (NCU). Calhoun Co., 10 mi. S of Blountstown, *Adams 700* (FLAS, FSU, GH, NY, SMU, VDB). Clay Co., 2.7 mi. S of Cove Springs along US Hwy. 17, *Raven 18686* (DS). Columbia Co., 3.6 mi. NE of Lake City, Osceola National Forest, *Perdue 1824* (C, FSU, GA, GH, NCU, SMU, TEX, USF). Duval Co., near Jacksonville, *Curtiss 924* (CM, F, FLAS, GA, GHM, MO, MSU, NY, US). Escambia Co., near Pensacola, *Burkhalter 2919* (FLAS). Franklin Co., 38.8 mi. W of jct. of US Hwys. 98 & 319, *Peng et al. 4345* (MO). Gadsden Co., ca. 3 mi. NW of Quincy along US Hwy. 90, *Webb & Ross 1011* (TENN). Gulf Co., between Weewahitchka & Port St. Joe, *Godfrey & Kral 54168* (DUKE, FSU, GH, NY, TEX, USF, VDB). Hamilton Co., 3 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Holmes Co., 4.1 mi. W of Ponce de Leon, *McDaniel 5206* (FSU). Jackson Co., 5 mi. E of Marianna, near Rd. 90, *Hood 2593* (FLAS). Jefferson Co., W of Wacissa along Tram Rd., along St. Marks River, *Godfrey 70908* (FSU). Leon Co., 6 mi. N-NE of Chaires, *Kral 3687* (FLAS, GA, GH, NY, S, SMU, TENN, UNA, USF). Liberty Co., just S of Gadsden Co. line on Rt. 267, near jct. with Rt. 20, *Anderson 4477* (FSU, MO). Madison Co., 6.8 mi. W of Greenville on US Hwy. 90, *Raven 18625* (DS). Okaloosa Co., E of Oakgrove, near Yellow River, by FL Rt. 2, *Godfrey 75427* (FSU). Santa Rosa Co., between I-10 & Milton, *Godfrey 73798* (FSU). Wakulla Co., 6.1 mi. N of Sopchoppy along FL Hwy. 375, *Wooten 2270* (FSU). Walton Co., 3 mi. W of jct. US Hwy. 331 on US Hwy. 98, near Santa Rosa Beach, *Raven 18594* (DS, NCU). Washington Co., 3.5 mi. E of Caryville, *Kral & Godfrey 5961* (FSU, USF). GEORGIA: Appling Co., near Baxley, s.d., *s.c. 923h* (US). Atkinson Co., ca. 5 mi. S of Pierson, Coastal Plain Province, *Duncan 3015* (GA, GH, US). Baker Co., ca. Big Cypress area, 1946, *Ford & Thorne s.n.* (TENN). Brooks Co., 17 mi. N of Madison, FL on GA Hwy. 33, *Ramsey & Stripling 153* (FSU, SMU). Bryan Co., S side of Richmond Hill, *Kral 18806* (VDB). Bulloch Co., 3.5 mi. from jct. of GA Rt. 67 & GA Rt. 119, in SE part of county, near church, *Boole 1198* (NCU). Camden Co., 6.6 mi. S of Woodbine on US Hwy. 17, *Raven 18701* (DS, FLAS). Charlton Co., GA Hwy. 94, between Moniac & St. George, *Jones et al. 23027* (GA). Chatham Co., near Savannah, s.d., *s.c. 4169C* (S, US). Colquitt Co., 4.8 mi. NW of Berlin, Coastal Plain Province, *Faircloth 2676* (NCU). Cook Co., 6 mi. W of Adel at the Porter Purvis Farm, Coastal Plain Province, *Faircloth 2401* (GA, NCU). Decatur Co., 1.5 mi. E of Climax, by US Rt. 84, *Godfrey 77562* (FSU). Dooly Co., 2 mi. N of Pinehurst turnoff, by I-75, *Kral 51610* (VDB). Early Co., W central boundary of Co. in Moccasin Pond, *Duncan 4025* (GA, MO,

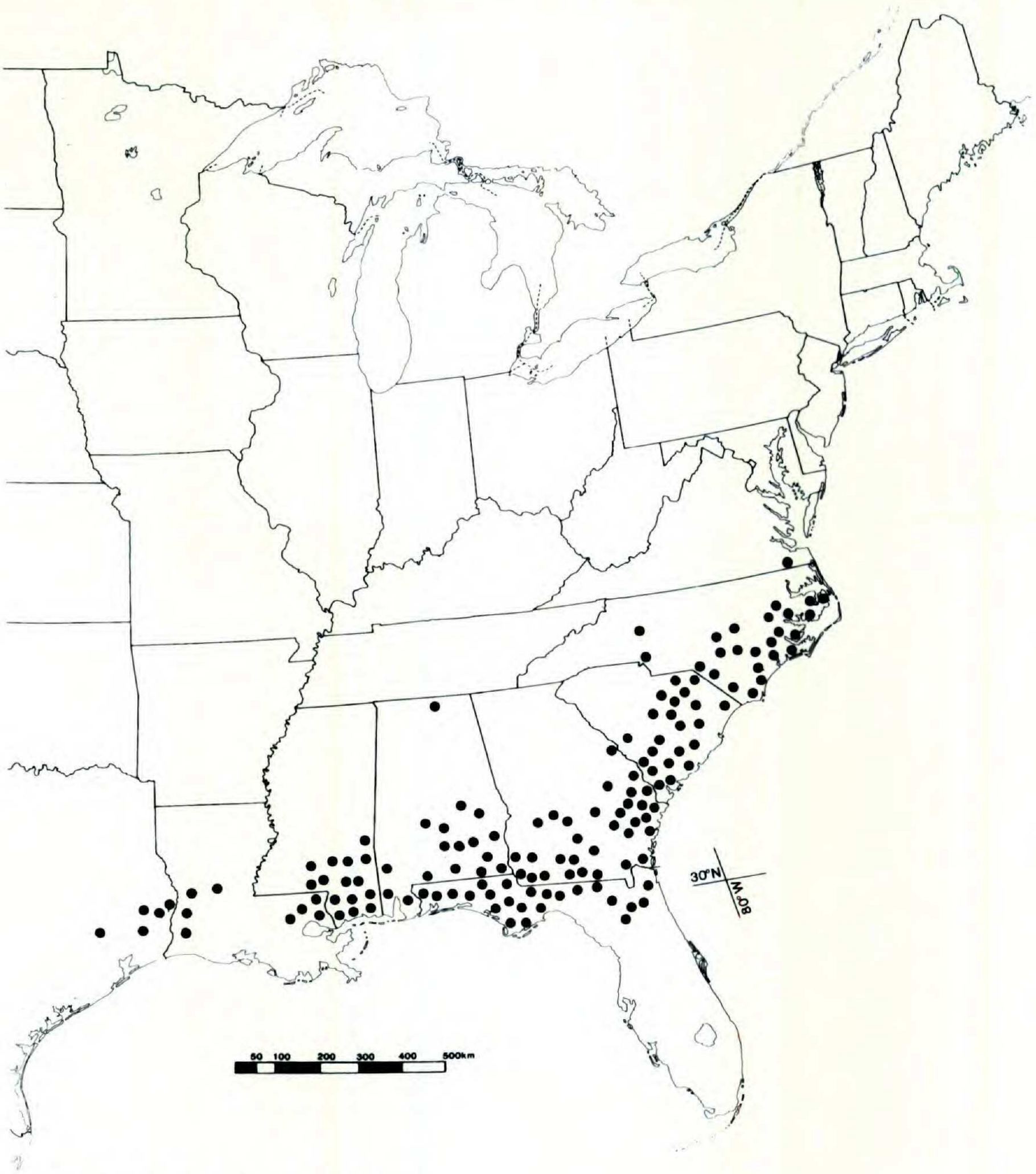

FIGURE 54. Distribution of *Ludwigia pilosa*.

SMU). Echols Co., 2.6 mi. E of Statenville, *Kral 51645* (VDB). Effingham Co., near Eden, 1875, *Curtiss s.n.* (US). Emanuel Co., 0.8 mi. S of I-16 on US 1 along the Ohoopee River, *Peng et al. 4024* (MO). Evans Co., 1 mi. S of jct. GA 169 & US 25 & 301, on US 25 & 301, *Peng et al. 4107* (MO). Grady Co., 3.5 mi. NW of Calvary on the J. R. Boyette property, *Faircloth 1510* (GA, MO, NCU). Irwin Co., 7.3 mi. SW of Irwinville at Tift–Irwin county line, *Faircloth 5408* (GA). Lanier Co., 2 mi. S of Lakeland, along GA Hwy. 31, *Thigpen et al. 226* (NCU). Liberty Co., near Hinesville, Camp Stewart, 1943, *Gumm s.n.* (C). Long Co., 4.2 mi. SE of Tattnall county line on US 301 & 25, *Peng et al. 4110* (MO). Lowndes Co., 7.3 mi. N of Valdosta, *Faircloth 2634* (GA, NCU). McIntosh Co., 2 mi. E of power line on Wesley Lake Rd., *Bozeman 2307* (GA, NCU). Richmond Co., Sanitary Dairy Pond, Augusta, 1924, *Hildebrand s.n.* (DUKE mixed with *L. pilosa* × *L. sphaerocarpa*). Screven Co., 7 mi. S of Sylvania, *Kral 22363* (VDB). Seminole Co., 1.5 mi. E of Donaldsonville, *Godfrey 63209* (FSU). Sumter Co., near Leslie, *Harper 591* (NY, US, W). Tattnall Co., 1.6 mi. N of Lane's Bridge, GA Hwy. 169, *Bozeman 5979* (NCU). Wayne Co., 5.8 mi. W-NW of Odum, *Duncan 23859* (FLAS, GA). Wheeler Co., 4.5 mi. W of Alamo, *Kral 22330* (VDB). Wilcox Co., 10.9 mi. N-NW of Abbeville, *Duncan & Hardin 14264* (GA, MISS, NCU, SMU, TENN, USF). LOUISIANA: Beauregard Parish, 6 mi. N of Singer, near Zion Church, *Thieret 28115* (FSU). Calcasieu Parish, 2.5 mi. W of Sulphur, just S of Stegall, *Thieret 20591* (DS, FSU). Livingston Parish, near Albany, *Rogers 2415-A* (NCU, SMU). Rapides Parish, near Alexandria, s.d., *Hale s.n.* (GH). St. Tammany Parish, just S of St. Tammany along Bayou Lacombe, *Thieret 21648* (DS, FSU). Tangipahoa Parish, 1 mi. W of Robert, *Correll & Correll 9288* (DUKE, FSU, ND). Vernon Parish, ca. 3.5 mi. E of Rosepine off LA 1146, *Allen & Vincent 651* (GA). Washington Parish, near Franklinton, *Demaree 46896* (MO, NO, SMU). MISSISSIPPI: Clarke Co., 1896, *Schuchert s.n.* (NY). Covington Co., S of Collins, Hwy. 49, *Jones 10908* (GA, MISS, NCU). Forrest Co., near Rayland Hills, *Rogers 4096* (MISS). George Co., near Agricola, *Demaree 32797* (DUKE, SMU, VDB). Hancock Co., 2 mi. NE of MS 603 on MS 43, *Peng et al. 4359* (MO). Harrison Co., near Handsboro, *Demaree 29713* (DUKE, NCU, SMU, TEX, VDB). Jackson Co., 2 mi. W of US 10 & MS 90, on MS 90, *Peng et al. 4354* (MO). Jones Co., 6.6 mi. NE of Moselle on MS Hwy. 11, *Raven 18568* (DS).

Lawrence Co., 2 mi. N of Monticello on Hwy. 270, *Jones 9976* (MISS). Marion Co., 0.8 mi. S of Sandy Hook on Hwy. 35, *Jones et al. 20280* (FSU, GA, MISS, VDB). Pearl River Co., 6 mi. NW of Poplarville, *Darwin et al. 729* (MO, NO). Perry Co., 5 mi. E of Runnelstown, *Jones 9599* (MISS). Stone Co., near McHenry, U. of Miss. Forest Lands, *Demaree 34056* (DS, SMU, USF). Walthall Co., N of Varnado, just over LA line on LA 21, *Kral 17394* (VDB). Wayne Co., 2.7 mi. E of county line, Hwy. 84, *Jones 9724* (MISS). NORTH CAROLINA: Beaufort Co., near Washington, *Sargent 54* (US). Brunswick Co., 0.2 mi. W of Longwood on NC 904, *Peng et al. 3886* (MO). Carteret Co., 0.25 mi. from Hwy. 70 on rd. to Harker's Island, *Blomquist 15572* (DUKE, VDB). Columbus Co., 2.7 mi. N of Wananish, *Fox & Whitford 1889* (FSU, NCSC, SMU). Craven Co., 6.3 mi. NE of Jones Co. line on county rd. 1100, *Peng et al. 3832* (MO). Cumberland Co., 1.5 mi. NE of Godwin, just E of Damat Rhode's pond, *Fox 5627* (FSU, NCSC, NY, SMU). Dare Co., just N of Manteo city limits, beside US 64, *Duke 54237* (NCU). Duplin Co., 0.7 mi. NW of Pin Hook, *Ahles 35840* (FLAS). Harnett Co., 8 mi. S-SW of Lillington on Anderson Creek at NC 210, *Beal 2702* (NSC). Hyde Co., 12 mi. W of Swan Quarter, *Oosting 30* (DUKE, FLAS). Iredell Co., near Statesville, s.d., *Hyanus s.n.* (MO). Johnston Co., E of Clayton, near jct. of NC Hwys. 96 & 42, *Radford 44388* (NCU). Jones Co., 0.4 mi. W of county rd. 1105 (Catfish Rd.), on Forest Service Rd. 172 (Mirey Branch Rd.) E-SE of Maysville off NC Rt. 58, *Peng et al. 3802* (MO). Martin Co., 1 mi. NW of Parmele, near US 64, *Radford 39337* (GH, NCU). Mecklenburg Co., near Smithsville, Oct., *s.c., s.n.* (NY). New Hanover Co., 1867, *Canby s.n.* (F, NY). Onslow Co., 5.5 mi. S of NC 41, on county rd. 1003, S of Comford, *Peng et al. 3791* (MO). Pamlico Co., 1.1 mi. W of Grantsboro, Goose Creek, *Beal 2521* (DUKE, NCSC). Pender Co., 1 mi. S of Ward's Creek on US 421, *Duke 6472* (NCU). Pitt Co., 400 yds. E of jct. of NC Hwys. 11 & 903, *Duke 54173* (NCU). Robeson Co., 2.6 mi. E of Daystrom on rd. to Philadelphus, *Ahles & Leisner 32962* (NY, VDB). Sampson Co., 0.9 mi. S of Halls Store, vicinity of Mill Pond, *Ahles & Leisner 33640* (NCU). Scotland Co., 4.7 mi. E-NE of Johns on rd. to Maxton, *Ahles 3700* (NCU). Tyrell Co., 1.5 mi. SE of Cross Landing, *Radford 42541* (NCU, USF). SOUTH CAROLINA: Aiken Co., 1969, *HWR s.n.* (US). Allendale Co., ca. 2 mi. W of Barton on County Rd. 23, *Bell 5106* (NCU). Bamberg Co., 0.7 mi. W of Olar on SC 64, then 0.8 mi. S on dirt rd. (SW of Olar), *Ahles 37683* (NCU). Beaufort Co., 5 mi. S of Hardeeville, *Eyles 4400* (GA). Berkeley Co., 10 mi. NW of Bonneau, *Godfrey & Tryon 1623* (GH, US). Charleston Co., 4.8 mi. E of SC 174 on US 17, E of Osborn, *Peng et al. 3908* (MO). Chesterfield Co., 3 mi. NW of Patrick, near SC 102, *Radford 15873* (NCU). Clarendon Co., 1 mi. S of Sandinia, Black River Swamp, *Godfrey & Tryon 1486* (F, GH, MO, NY, TENN, US). Colleton Co., 4.2 mi. E of Smoaks, *Raven 18717* (DS). Darlington Co., across lake from Hartsville, *Smith 35* (NCU). Dorchester Co., 1.5 mi. N-NE of St. George on US 15, *Ahles & Haesloop 37776* (NCU). Horry Co., on SC Hwy. 9, 3 mi. NW of jct. US Hwy. 17, *Dille & Dille 342* (MO). Jasper Co., 2.5 mi. N of SC 46 on US 17, N of Hardeeville, *Peng et al. 3973a* (MO). Richland Co., 7 mi. SE of Columbia, *Smith 860* (GH). Florence Co., forest at N limits of Scranton, *Raven 20456* (DS). Hampton Co., 1.8 mi. NW of Yemassee on SC 28, *Ahles & Bell 18351* (NCU). Horry Co., 2 mi. N of Little River, beside Hwy. 905, *Duke 54115* (NCU). Jasper Co., 2.5 mi. N of SC Hwy. 46 on US Hwy. 17, N of Hardeeville, *Peng et al. 3973-a* (MO). Kershaw Co., 4.5 mi. SE of Bethune, near Lynches River, *Radford 27737* (NCU). Lee Co., 6 mi. W of Bishopville, near SC 34, Scape Ore Swamp, *Radford 29437* (NCU). Marlboro Co., 1.5 mi. E of Wallace, near SC 90, *Radford 15626* (NCU). Orangeburg Co., *Eggleston 5025* (GH, MO, NY). Sumter Co., 15 mi. E of Mayeville, near SC 53 & Lynches River, *Radford 27561* (NCU). Williamsburg Co., 3.5 mi. S of Andrews, *Kral 19168* (VDB). TEXAS: Hardin Co., 2 mi. N of Gist, *Cory 50923* (GH, NY, SMU). Jasper Co., 20 mi. NW of Jasper, *Correll 28573* (TEX). Montgomery Co., just W of Fostoria, *Correll 33994* (GH, TEX). Newton Co., 1.5 mi. E of Kirbyville, State Forest No. 1, *Cory 49815* (DS, GH, NY, SMU, US). Tyler Co., ca. 3.5 mi. S of Warren, Hyatt Lake Estates, *Correll & Correll 36729* (TEX). VIRGINIA: Nansemond Co., S of Baines Hill School, Adams Swamp, *Fernald & Long 13705* (C, GA, GH, MO, TENN).

Ludwigia pilosa is a distinctive species in sect. *Microcarpium* characterized by being densely hirtellous throughout; reddish brown leaf midveins especially abaxially; sepals elongate-triangular, creamy, and often tinged with pink, reflexed at the tips; and capsules subglobose to somewhat oblong-obovoid, with a pair of long bracteoles attached slightly above the base. The only species that has consistently been confused with *L. pilosa* is the recently named *L. ravenii* (Peng, 1984). The similarity in these two species is in aspect and in the vestiture. They differ in many other characters, notably floral parts and breeding systems. *Ludwigia ravenii* is modally autogamous, with obscure greenish sepals, and all of its floral parts are significantly smaller than those of *L. pilosa*. Further, the seed surface cells are transversely elongate rather than subisodiametric.

The flowers of *Ludwigia pilosa*, in contrast, are unable to undergo mechanical self-pollination. Their showy sepals and copious nectar, which is produced by the nectary disc, unfailingly attract various insect visitors such as ants, wasps, bumblebees, honeybees, and moths to effect pollination. *Ludwigia pilosa* grows with diploid *L. linifolia*, *L. microcarpa*, tetraploid *L. glandulosa*, *L. lanceolata*, *L. ravenii*, *L. sphaerocarpa*, *L. suffruticosa*, and the hexaploid *L. alata*, which is closely allied to the tetraploid species group. It forms fertile hybrids with probably all tetraploid species and with *L. alata* when they grow together. Natural hybrids between *L. pilosa* and *L. ravenii* are presumably rare (*L. ravenii* is rare itself) and difficult to detect. An intersectional hybrid between *L. pilosa* and *L. arcuata* ($n = 16$; sect. *Dantia*) was found in Mobile Co., Alabama (Peng, 1988). All natural hybrids are intermediate morphologically, having vestiture similar to that of *L. pilosa* but shorter and other

features diagnostic of the other putative parents (e.g., the winged fruits of *L. lanceolata*, elongate capsules of *L. glandulosa*, and additional features). Two such hybrids have previously been named: *L. capitata β pubens* Torrey & A. Gray (= *L. pilosa* × *L. suffruticosa*) and *L. simulata* Small (= *L. pilosa* × *L. lanceolata*). Kral (1976) reported a range extension of *L. polycarpa* to Alabama, based, in fact, on a natural hybrid population of *L. pilosa* × *L. glandulosa*. The only species that hybridizes extensively with *L. pilosa* and produces many hybrid swarms or introgressed populations is *L. sphaerocarpa*. Plants of these populations exhibit a varying degree of intermediacy between the two species. They are discussed further under *L. sphaerocarpa*.

Hybrids between *Ludwigia pilosa* and the other tetraploid species or the hexaploid *L. alata* are readily synthesized in the experimental greenhouse and are quite fertile. It is generally difficult to obtain hybrids between *L. pilosa* and diploid species or the *L. curtissii* complex. Floriferous and vigorous hybrids of *L. pilosa* × *L. linifolia* and *L. pilosa* × *L. curtissii*, however, were obtained. Seed set was nonexistent or negligible in these hybrids.

11. Ludwigia ravenii Peng, Syst. Bot. 9: 129. 1984. TYPE: U.S.A. South Carolina: Berkeley Co., 0.1–0.2 mi. SW of jct. of Co. 16 and Co. 6, on Co. 16 W of Moncks Corner, scattered in roadside sedgy, sandy ditch, on loam densely covered by *Sphagnum subsecundatum* Nees, associated with *Cyperus, Xyris, Eriocaulon, Paspalum, Panicum, Hypericum, Polygonum, Rhexia, Liatris, Eupatorium, Ludwigia linearis* Walter, *L. hirtella* Raf., 9 Sep. 1982, *Ching-I Peng 4402* (holotype, MO-3041593; isotypes, B, BM, DAO, DUKE, F, FLAS, FSU, FTG, GA, GH, HAST, KYO, LE, MISS, MISSA, MO, NCSC, NCU, NY, P, PE, TAI, TAIF, TENN, TI, US, USF, VDB). Figure 55.

Plants densely hirtellous throughout. Stems erect, usually well branched and leafy, (15–)35–90 cm tall, densely hirtellous, the hairs 0.3–0.6(–0.75) mm long; aerenchyma (if any) slightly developed, in lower stems. Stolons slender, several from the base, to 18 cm long, 0.6–1.5 mm thick, glabrous or hirtellous, occasionally bearing flowers and fruits, the leaves purplish, elliptic to rotund, 10–18 mm long, 6–14 mm wide, apex rotund to acute, base attenuate into a petiole 1–3 mm long. Cauline leaves pale green on both surfaces, narrowly lance-elliptic, 13–65 mm long, 4–15 mm wide, densely hirtellous on both surfaces, the hairs 0.2–0.5 mm long, apex acute, margin entire with minute hydathodal glands, base attenuate into narrowly winged petiole 1–8 mm long. Stipules reddish purple, lanceolate to widely deltate, succulent, 0.25–0.45 mm long, 0.15–0.25 mm wide. Flowers many, in leaf axils, not congested. Sepals green on both surfaces, broadly ovate-deltate, 1.5–3 mm long, 1.4–2.1 mm wide, densely hirtellous without, glabrous within, apex acuminate, margin entire. Petals 0. Anthers 0.3–0.35 mm long, 0.4–0.5 mm wide; filaments 0.7–1.1 mm long. Pollen grains shed as tetrads. Nectary disc greenish, raised 0.3–0.4 mm on ovary apex, 1.4–2.5 mm across, 4-lobed, glabrous. Style 0.25–0.5 mm long, glabrous; stigma subglobose, 0.25–0.45 mm across. Mature capsules oblong-obovoid, obconical when young, (3–)4–5(–5.3) mm long, 2–3.5(–4) mm thick, densely hirtellous, pedicels 0.2–0.5 mm long. Bracteoles attached near capsule base, lanceolate or elliptic to very narrowly so, (1.5–)2–4.3 mm long, 0.25–0.9 mm wide, hirtellous. Seeds light brown, elliptic-oblong with slightly curved ends, 0.5–0.7 mm long, 0.25–0.35 mm thick, pluriseriate in each locule, free, the surface cells elongate transversely to the seed length. Self-compatible and modally autogamous. Gametic chromosome number, $n = 16$.

Distribution. *Ludwigia ravenii* occurs in wet, peaty habitats, such as ditches or margins of ponds, bogs, and swamps. It is found as scattered populations in coastal southeastern Virginia, eastern North Carolina, and southeastern South Carolina and with somewhat disjunct populations in northeastern Florida (Fig. 56). Flowering from July to September; fruiting from August to October.

Specimens examined are cited in full in Peng (1984).

This recently discovered species consists of scattered, morphologically very uniform populations. Owing to its densely hirtellous vestiture and relative rareness, it was previously not well understood and was confused with *Ludwigia pilosa*, the only other species of sect. *Microcarpium* that is consistently densely hirtellous; that species, however, is widespread and common. As was shown in the table comparing *L. ravenii* with related species (Peng, 1984), *L. ravenii* is very distinct from *L. pilosa*.

Ludwigia ravenii has small inconspicuous flowers with greenish sepals and short stamens and styles. Its anthers are firmly appressed to the stigma shortly after anthesis. These characteristics strongly suggest that it is modally autogamous. This was corroborated by my field study at the type

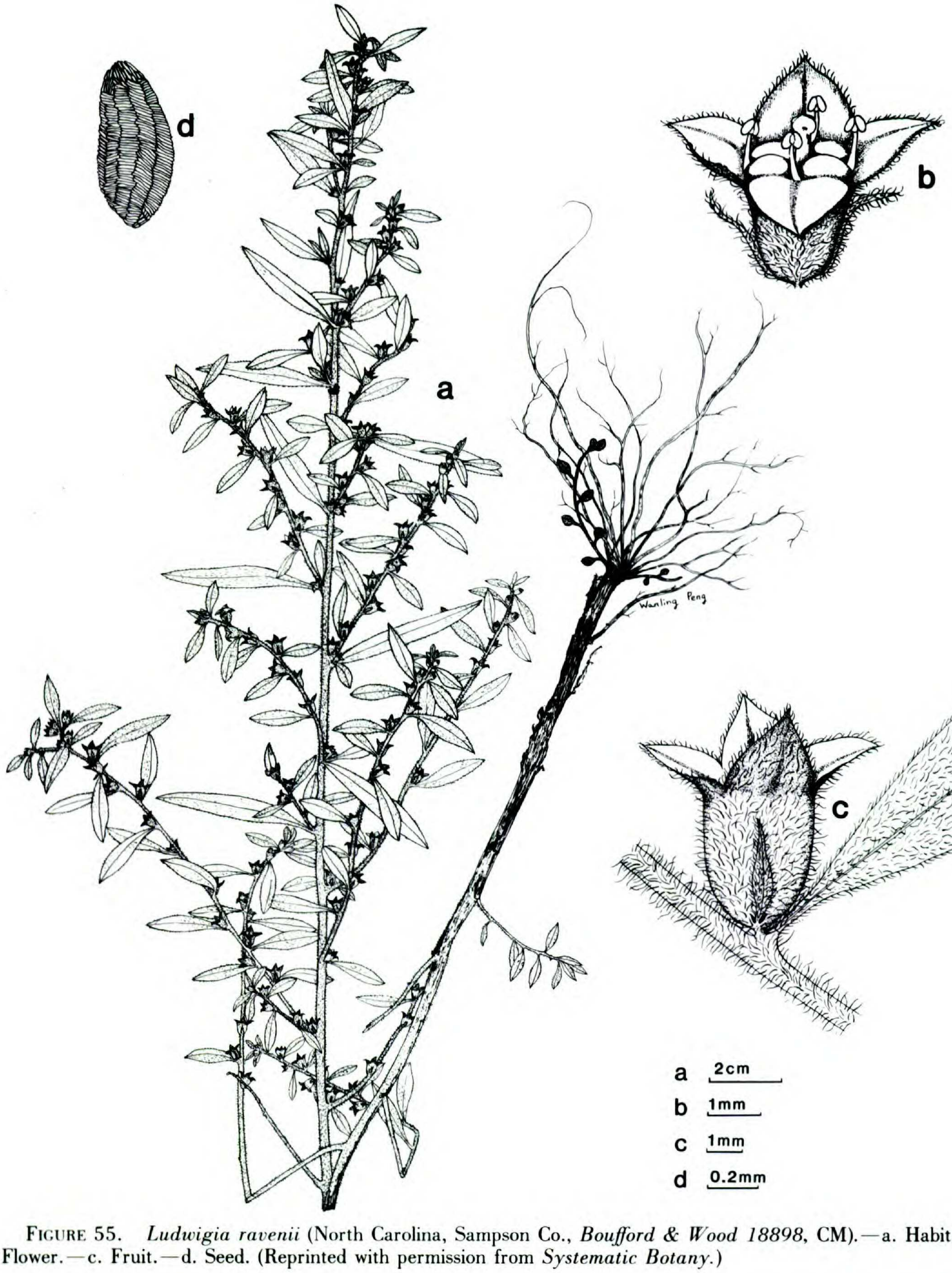

FIGURE 55. *Ludwigia ravenii* (North Carolina, Sampson Co., *Boufford & Wood 18898*, CM).—a. Habit.—b. Flower.—c. Fruit.—d. Seed. (Reprinted with permission from *Systematic Botany*.)

locality (Peng, 1984): for two hours by the ditch where *L. ravenii* grew, I did not observe any insect visitors, whereas 0.5 mi. away in the same ditch, I witnessed a swarm of honeybees visiting and hovering over flowers of a population of *L. pilosa*.

Ludwigia ravenii does not appear to grow aggressively. It starts to form stolons only late in its fruiting season (September to October). Unlike most other tetraploid members of sect. *Microcarpium*, these stolons are usually slender and short, resembling those of *L. microcarpa*. Consequently, the populations consist of scattered individuals instead of large colonies connected by stolons, as is typical in *L. pilosa* and other species.

Live plants of *Ludwigia ravenii* were not collected until after the completion of my biosystematic study of *Ludwigia* sect. *Microcarpium*, so its genetic relationships with the other tetraploid

FIGURE 56. Distribution of *Ludwigia ravenii*.

members of the section remain obscure. The extensive crossing data already available for other species clearly demonstrate, however, that pollen stainability and seed set are high in hybrids between any two tetraploid species, no matter how different morphologically they are (Peng, 1988). Circumstantial evidence thus suggests that *L. ravenii* is almost certainly interfertile with other species of the tetraploid group of sect. *Microcarpium*.

12. Ludwigia microcarpa Michaux, Fl. Bor.-Am. 1: 88. 1803. *Isnardia microcarpa* (Michaux) Poiret in Lam., Encycl. Suppl. 3: 188. 1813. LECTOTYPE: U.S.A. South Carolina: Berkeley Co., Goose Creek, wet places, 1785–1796, *A. Michaux s.n.* (lectotype, P; photograph, MO; here selected). Figure 57.

Plants glabrous, varied in habit, ranging from erect, unbranched, slender herbs to being profusely branched with somewhat woody bases. Stems erect or ascending, rarely prostrate and rooting at the nodes, 5–60 cm tall, 0.4–1.5(–4) mm thick, the leaf bases distinctly decurrent, with or without aerenchyma at stem base. Stolons pinkish, several from base, slender, 4–15(–25) cm long, 0.4–0.75 mm thick, the leaves broadly elliptic to suborbicular, 2.2–6.6 mm long, 2.2–5.2 mm wide, petioles 1.5–5 mm long. Cauline leaves obovate-spatulate or oblanceolate, sometimes narrowly oblance-elliptic, 4–17 mm long, 1.5–10 mm wide, glabrous, apex acute or mucronate, margin subentire, with prominent hydathodal glands forming minute teeth, minutely papillose-strigillose, the hairs ca. 0.05 mm long, occasionally smooth, base attenuate into winged petioles 0.5–5 mm long; main veins on each side of the midrib 3–4, obscure adaxially, conspicuous and slightly raised abaxially; branch leaves sometimes remarkably smaller than main cauline leaves. Stipules reddish purple, lanceolate-deltate, succulent, ca. 0.13–0.15 mm long, 0.1–0.13 mm wide. Flowers axillary, usually not crowd-

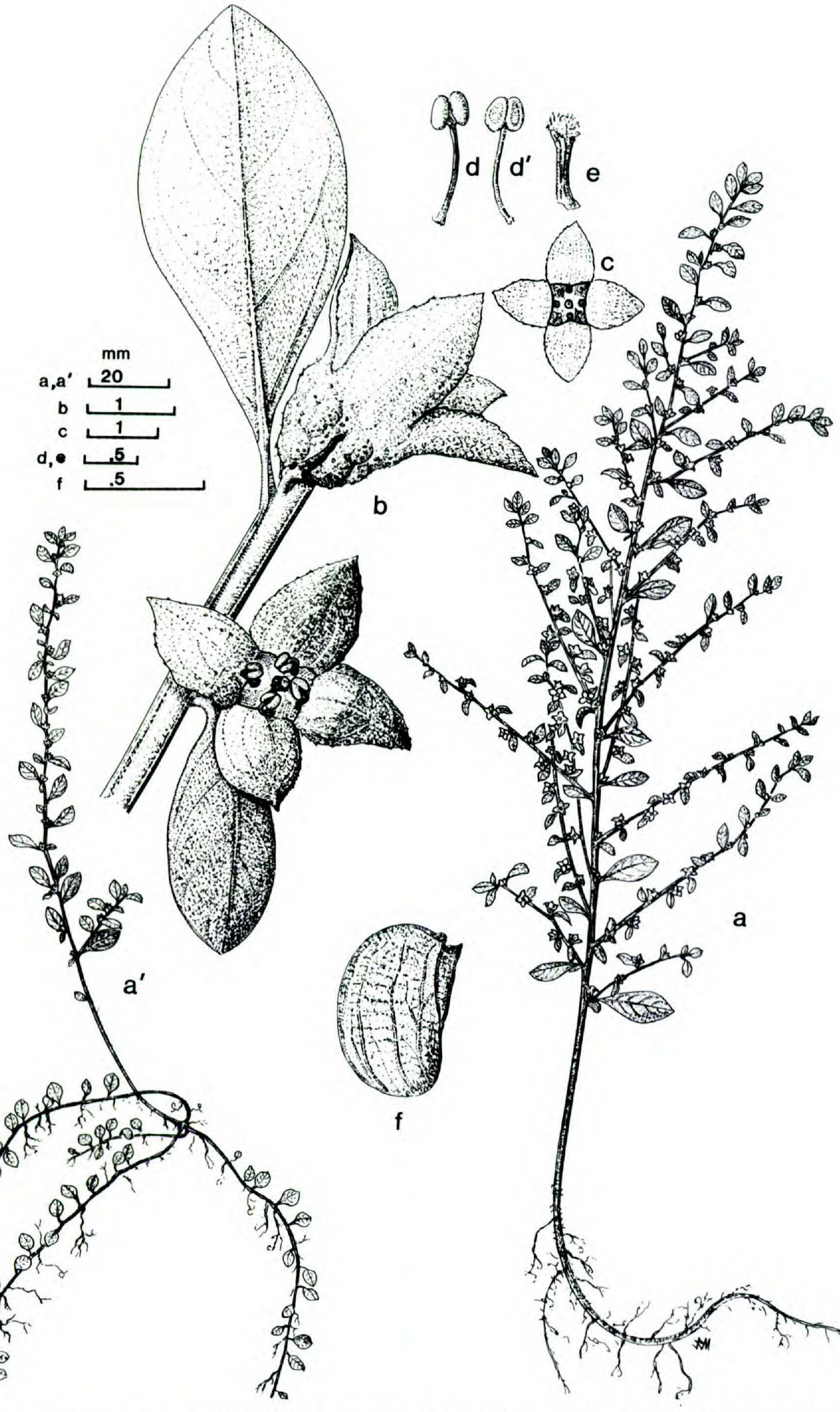

FIGURE 57. *Ludwigia microcarpa*. All but a′ from Florida (Monroe Co., *Godfrey 63525*, MO); a′ from North Carolina (Brunswick Co., *Leonard & Moore 7579*, MO).—a. Habit, showing erect stem.—a′. Erect plant with basal stolons.—b. Portion of branch with flower and fruit.—c. Top view of fruit.—d, d′. Adaxial and abaxial views of stamen.—e. Stigma and style with pollen on stigma.—f. Seed.

ed. Sepa is green with whitish, thickened base, ascending in flower and spreading in fruit, ovate-deltate, 0.9–2 mm long, 1–1.85 mm wide, glabrous, apex acuminate, margin remotely minutely papillose-strigillose, occasionally smooth. Petals 0. Anthers 0.1–0.2 mm long; filaments translucent, 0.4–0.55 mm long. Pollen grains shed singly. Nectary disc greenish, nearly flat on ovary apex, 0.5–1.2 mm across, 4-lobed, these represented by 4 greenish rhomboid spots, alternating with 4 smaller, rounded reddish scars of anther base on top of the mature capsule, glabrous. Style pale green, 0.25–0.4 mm long, glabrous; stigma green, subglobose, ca. 0.05–0.1 mm thick. Capsules obconical, 1–1.5 mm long, 1.4–1.9 mm thick, minutely puberulent, the hairs ca. 0.05 mm long, thin-walled, containing 6–20 seeds, these sometimes recognizable from outside as bumps, sessile or with pedicels up to 0.15 mm long. Bracteoles flanking capsule base, sublinear or narrowly oblong, 0.35–1.2(–1.5) mm long, 0.1–0.4 mm wide, usually with a swollen base, glabrous. Seeds dark reddish, ovate-oblong, 0.5–0.55 mm long, 0.3–0.4 mm thick, the surface cells transversely elongate, glabrous or sometimes densely covered by strigillose hairs (waxes?). Self-compatible and modally autogamous. Gametic chromosome number, $n = 8$.

Distribution. Plants of *Ludwigia microcarpa* grow in roadside ditches, marshes, ponds and streams at the borders, low meadows, low areas in open woods, edges of swamp forests, brackish marshes, hammocks, and solution pits of limestone on marl prairies. This species occurs along the Atlantic coast of North and South Carolina and Georgia, and throughout the Florida peninsula. It extends westward across the panhandle of Florida, southern Alabama, reaching southern Mississippi, with a single population in southwestern Louisiana. To the north, *L. microcarpa* occurs through western Georgia and central and western Alabama to southcentral Tennessee. Scattered populations are found in northcentral North Carolina and southcentral Missouri (Fig. 58). Furthermore, *L. microcarpa* occurs on several Caribbean islands, including the Bahamas, Cuba, and Jamaica. Flowering and fruiting throughout the year.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., River Styx E of Mobile on US 90, *Kral 35805* (MSC, VDB). Bibb Co., ca. 7 mi. N Centerville by Co. 27, *Kral 47928* (VDB). Calhoun Co., 5.5 mi. W Piedmont on US 278, *Kral 37736* (VDB). Cherokee Co., US 411, 2 mi. W of Centre, *Kral 31769* (GA, NCU, SMU, VDB). Chilton Co., I-65, ca. 9 mi. N of Clanton and AL 22, *Kral 53296* (VDB). Clarke Co., on Co. 19, N of Choctaw Bluff, *Kral 35473* (NY, VDB). Conecuh Co., ca. 4 mi. NE of Lenox, *Kral 40954* (VDB). Covington Co., 2 mi. W of Opp, *Kral 20622* (VDB). Geneva Co., W side of Geneva, *Kral 32026* (FSU, SMU, VDB). Houston Co., Chattahoochee State Park, *Godfrey 75953* (FSU). Morgan Co., ca. 4 mi. S of Decatur, *Kral 33465* (C, SMU, VDB). St. Clair Co., ca. 3 mi. NW of Asheville, by US 231, *Kral 32361* (NCU, SMU, VDB). FLORIDA: Alachua Co., Gainesville, 1938, *Arnold & West s.n.* (DUKE, FLAS). Bay Co., 1 mi. N of Panama City, FL 77, *Godfrey 75318* (MO). Broward Co., S of Wiles Road, 1.4 mi. W of US 441, ca. 3 mi. N of Margate, 1964, *Will s.n.* (FLAS, FSU). Calhoun Co., banks of Chipola River, Wofaltha, *Godfrey 57758* (FSU, GH). Charlotte Co., Punta Gorda city, on US Hwy. 41, ca. 1 mi. S of jct. of US Hwys. 17 & 41, *Peng et al. 4294* (MO). Citrus Co., 5 mi. S Homosassa, *Kral 7770* (GH, US). Clay Co., 5 mi. W of Penny Farms on FL Hwy. 16, *Peng et al. 4161* (MO). Collier Co., on FL Hwy. 82, 1.2 mi. N of C-890; 5.7 mi. E of Hendry county line, *Peng et al. 4281* (MO). Columbia Co., Camp O'Leno, *Beck 243* (FLAS). Dade Co., 25 mi. W of FL Hwy. 27, on US Hwy. 41, *Peng et al. 4217b* (MO). Dixie Co., 4 mi. NW of Cross City, *Godfrey 56021* (CM, DS, DUKE, GH, LL, MO, MSU, NCU, NY, SMU, TENN). Duval Co., FL Hwy. 13, 1.1 mi. N of Interstate 295, *Peng et al. 4147* (MO). Escambia Co., Pensacola, *Godfrey 74408* (FSU, NCU, MO). Franklin Co., 41.7 mi. W of jct. (the one that is closer to Teresa Beach) of US Hwys. 98 & 319, *Peng et al. 4348* (MO). Gulf Co., 3 mi. S of Port St. Joe, *Kral & Kral 7191* (FLAS, GH, US, USF). Hendry Co., along FL 29, about 3 mi. S of La Belle, *Henderson 63-1611* (FSU). Hernando Co., 3 mi. W of Weeki Wachee Springs, *Kral & Kral 7029* (FLAS, GA, GH, NY, USF). Hillsborough Co., 2.8 mi. N of FL Hwy. 582, on E side of FL Hwy. 581, *Peng et al. 4332* (MO). Holmes Co., 1 mi. W of Wentville, *Kral & Redfearn 2885* (FSU, GH, NCU). Indian River Co., canal margins 10 mi. W of Vero Beach, *Kral 4942* (FSU, VDB). Jackson Co., Lake Seminole, N of Sneads, *Godfrey & Houk 61399* (FSU, NCU, SMU). Lake Co., 3.7 mi. S of Mascotte city limit, on county rd. 33, *Peng et al. 4166* (MO). Lee Co., 3.8 mi. S of Gladiolus Dr. (865) on San Carlos Blvd. (865), *Peng et al. 4288* (MO). Leon Co., Ochlockonee River W of Tallahassee, *Godfrey 73131* (FSU, MO, NCU, TENN). Levy Co., 0.5 mi. S of Gulf Hammock, *Kral & Kral 6963* (FLAS, GA, GH, USF). Liberty Co., 3.3 mi. E of FL 65 on FL 20, *Boufford et al. 18407* (MO). Madison Co., 2.6 mi. W of the Aucilla River on US 90, *Boufford & Ahles 9554* (CM, MO). Manatee Co., US 301 2 mi. N of Sarasota, *Raven 18657* (DS). Marion Co., Eureka, *Godfrey 60141* (FSU, MSU). Martin Co., 4.3 mi. E of Okeechobee and Martin Co. line, on FL Hwy. 710, at Brady Ranch, between RR and Hwy., *Peng et al. 4200* (MO). Monroe Co., along rd. to Watson Hammock; Big Pine Key, *Killip 44291* (DS, FLAS, GA, GH, NY). Osceola Co., N of FL 532, ca. 1.5 mi. E of Interstate 4, *Wunderlin & Shuey 5829* (USF). Palm Beach Co., NW of Loxahatchee in the Corbitt Wildlife Mgmt. area, *Kral 5634* (FSU, SMU, VDB). Pasco Co., Aripeka, *Godfrey 57244* (FSU). Pinellas Co., along FL 580, ca. 1 mi. E of its jct. with US 19, *Henderson 63-1540* (FSU, JE, TEX). Polk Co., along US 192, just inside the county line, at the edge of Davenport, *Henderson 63-1632* (FSU). Putnam Co., 2.5 mi. S of San Mateo, *Godfrey & Reinhert 61131* (FSU). St. Johns Co., 1.9 mi. N of jct. of FL Hwy. 207 & C-305, on FL Hwy. 207, *Peng et al. 4156* (MO). Sarasota Co., on FL Hwy.

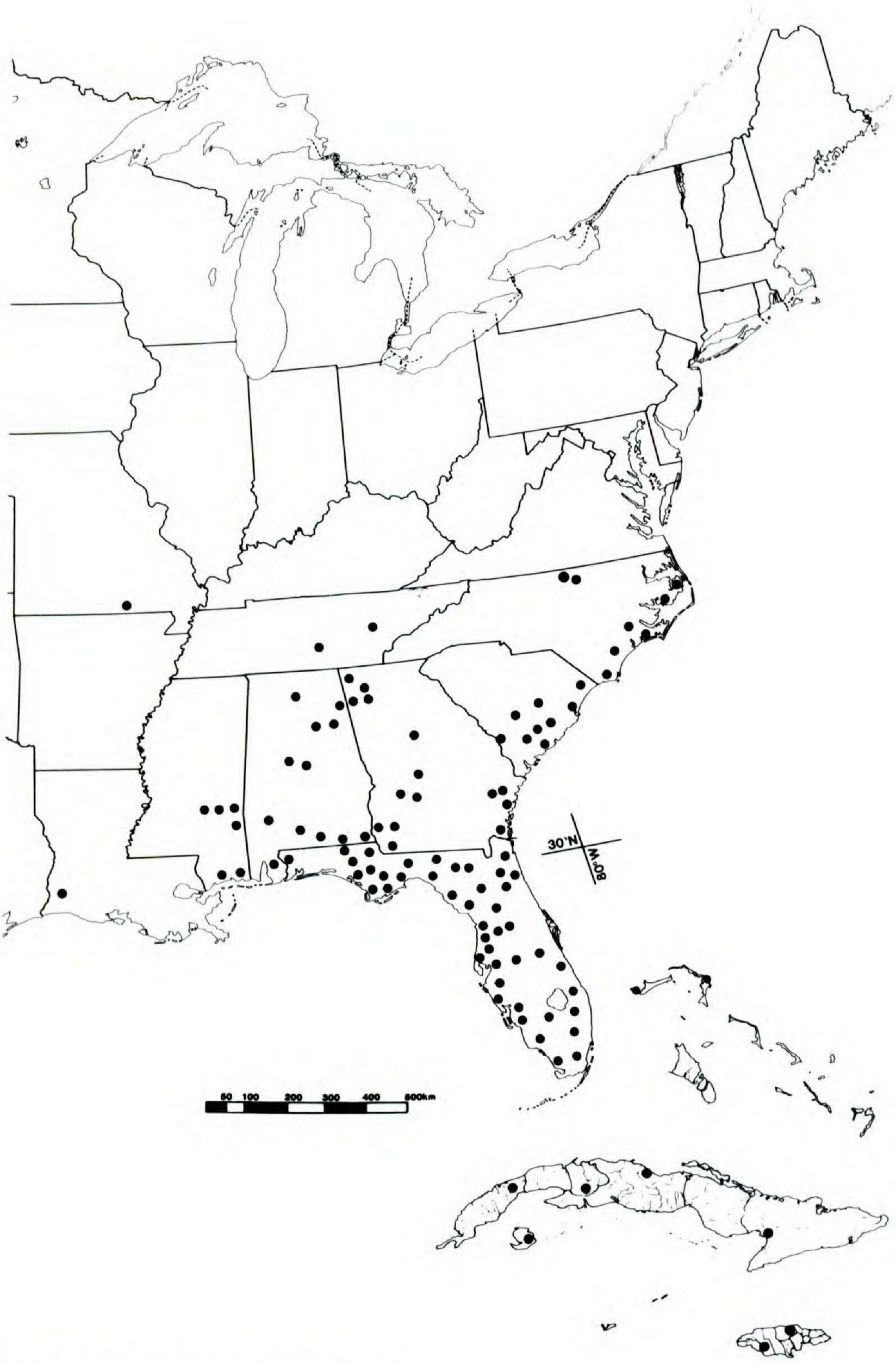

FIGURE 58. Distribution of *Ludwigia microcarpa*.

72, 0.5 mi. E of W boundary of Myakka River State Park, *Peng et al. 4313* (MO). Sumter Co., Bushnell, 14 mi. S of Rt. 301, *Sargent 6728* (SMU). Suwannee Co., Mayhaw ponds 5 mi. W of O'Brien, 1946, *West & Arnold s.n.* (FLAS). Taylor Co., on US Hwy. 98, 3.9 mi. W of jct. of US 27, 19 & 98 (Perry), *Peng et al. 336* (MO). Wakulla Co., 2 mi. N of St. Marks, *Raven 18601* (DS, NCU, USF). Washington Co., Alligator Creek, Rt. 90, W of Chipley, *Hood 2927* (FLAS). GEORGIA: Baker Co., Ivey's Mill Pond, *Eyles 7183* (DUKE, GA). Bartow Co., at edge of broad swampy runway from large spring S of Aubrey Lake, 5.6 mi., N12′ E of Cartersville, *Harris & Duncan 12797* (DUKE, FLAS, GA, GH, NCU, SMU, TENN, US, USF, VDB). Camden Co., 6.6 mi. S of Woodbine on US 17, *Raven 18703* (DS, NCU). Crisp Co., pond near Flint River, W of Cordele, *Eyles 6612* (GA). Decatur Co., along Spring Creek below dam, lots 30 and 31, District 21, *Thorne & Davidson 17267* (GA). Early Co., Cohelee Creek, 2 mi. NW of Hilton, *Duncan 6808* (GA). Floyd Co., 4.7 mi. N5′ W of Cave Springs, *Venard & Duncan 13114* (GA). Gordon Co., 1 mi. N of Fairmont, *Duncan 7219* (GA, MISS). Houston Co., 14 mi. S of Hawkinsville, *Svenson 6982* (TENN). Jasper Co., Monticello, 1846, *Porter s.n.* (GH, NY). Liberty Co., N of Liberty Co. line, S of Hinesville, *Kral 18859* (VDB). Long Co., 1.4 mi. SW of jct. of US Hwys. 301 & 25, and GA Hwy. 99, on US Hwys. 301 & 26, along Altamaha River, *Peng et al. 4127* (MO). McIntosh Co., 0.4 mi. NW of

jct. of Cox Rd. and GA Hwy. 251, on Cox Rd., *Peng et al. 4133* (MO). Sumter Co., in pine barrens, *Harper 471* (F, GH, MO, NY, US). Walker Co., Chickamauga, s.d., *s.c. 2671a* (US). LOUISIANA: Calcasieu Parish, vicinity of Lake Charles, *Mackenzie 426* (F, MO, NCU, NY). MISSOURI: Oregon Co., Hatcher's Spring in valley of Greer Spring branch, 1 mi. N of Greer, *Steyermark 27987* (F, GH). MISSISSIPPI: Clarke Co., Jackson Prairie, 1.5 mi. S-SW of Pachuta, *Jones & Jones 14614* (FSU, GA, MISS, NCU, USF, VDB). Harrison Co., ca. 4 mi. N of Biloxi, *Rogers 6780* (GH, NCU, NY). Jackson Co., 1 mi. N of Franklin Creek Church, ca. 5 mi. NE of Orange Grove, *Jones & Catchot 17421* (GA, MISS, TENN, USF). Jasper Co., 9 mi. N of Montrose, *McDaniel 2631* (NY, UNA). Smith Co., ca. 4.5 mi. W of Bay Springs, *Rogers 46028* (TENN). Wayne Co., Waynesboro, *Pollard 1215* (F, GH, MO, NY, US). NORTH CAROLINA: Brunswick Co., roadside ditch along SR 1335, 3.3 mi. SE of SR 1333, *Leonard & Moore 7579* (MO). Carteret Co., SE of Mullet Pond on Shackleford Banks, *Anderson 414* (DUKE, FSU, SMU). Dare Co., near Friscoe, *Radford 45093* (C, CM, E, FLAS, MISS, NCU, S, SMU, TENN, TEX, U, UNA, US, USCH, WCUH). Granville Co., Camp Butner, *Batson 1075* (DUKE, NY). Hyde Co., Ocracoke Isl., *Kearney 2323* (US). Jones Co., 0.4 mi. W of county rd. 1105 (Catfish Rd.), on Forest Service Rd. 172 (Mirey Branch Rd.), E-SE of Maysville of NC Hwy. 58, *Peng et al. 4800* (MO). Pender Co., 0.4 mi. N of county road 1593 and 7.3 mi. N of the New Hanover Co. line; on US Hwy. 17, N of Hampstead, *Peng et al. 4877* (MO). Person Co., Wheeley's Ch., *Batson 1074* (DUKE). SOUTH CAROLINA: Allendale Co., pond on S-3-26, 6.1 mi. S of jct. with US 301, 0.3 mi. N of jct. with S-3-41, *Radford et al. 11417* (DS, NCU). Berkeley Co., along railroad tracks, Moncks Corner, *Bradley & Blaisdell 3406* (BOON, NCU). Charleston Co., 24.5 mi. N of SC Hwy. 41 on US Hwy. 17, vicinity of Buck Hill Recreation Area, S of McClellanville, *Peng et al. 4897* (MO). Clarendon Co., Santee Reservoir, 2.8 mi. S of Jordan, *Radford 31050* (GH, NCU, NY, VDB). Colleton Co., 2.2 mi. NW of Canadys on SC 61, *Ahles & Bell 17888* (FSU, GA, NCU, USF). Dorchester Co., 2.9 mi. N of Rosinville on US 15, *Ahles & Baird 54898* (NCU). Georgetown Co., 8 mi. N of Georgetown, *Godfrey & Tryon 1043* (DUKE, F, GH, MO, NY, TENN, US). Horry Co., cart road across sand plain behind dunes, Myrtle Beach, *Godfrey & Tryon 1163* (CAS, DUKE, F, GH, MO, NY, TENN, US). Orangeburg Co., Branchville, s.d., *s.c. 2671c* (US). TENNESSEE: Coffee Co., 3.5 mi. SE of Manchester, on US 41, *Kral 26038* (FSU, VDB). Roane Co., shoreline of the Tennessee River, E of Thief Neck Isl., ca. 8 mi. SW of Kingston, *Wofford & Dennis 51043* (TENN, VDB). Union Co., stream bed of Little Barnes Creek, *Underwood 385* (TENN). BAHAMAS: Great Abaco Co., along Abaco camp road, S of Marsh Harbour, *Correll & Sauleda 50684* (IJ, MO). Great Abaco Isl., along Forest Drive, about 1.5 mi. NW of Marsh Harbour, *Correll & Meyer 44598* (F, FTG, NY, SMU, US). Grand Bahama Isl., Dead Man's Reef, 9 mi. E-SE of West End, *Lewis 7110* (FTG, NY). CUBA. HABANA PROV.: Laguna Ariguanabo, *León 8724* (GH, NY). ISLE OF PINES: San Juan, *Britton et al. 5527* (CM, F, GH, MO, NY). LAS VILLAS: Santa Clara, Caibatten, at Delores, *Ekman 16316* (S). MATANZAS: Tagüey Grande, at Babujales, *Ekman 16955* (F, G, NY, S, US). Province not known: La Magdalena, Cayamas, *Baker 4648* (POM). Cuba, *Wright 2554* (G). JAMAICA. SAINT ANN PARISH: Moneague, *Prior 902* (US); E side of the Black River Morass, ca. 1 mi. N of Mountainside, *Proctor 19694* (A, IJ, NY); Slipe District, *Proctor 33464* (IJ, RSA); *Proctor 27748* (IJ).

Ludwigia microcarpa is the only diploid species of sect. *Microcarpium* that is apetalous and has more or less spatulate leaves. It has the smallest stature, leaves, flowers, and fruits and has the fewest seeds (ca. 10–20) per capsule of any species in the section. Occasionally it may be confused with plants of the "*L. curtissii* complex" (including a hexaploid, *L. simpsonii*, and an octoploid, *L. curtissii*), which have similarly spatulate leaves and turbinate fruits. It is, however, distinguishable from the "*L. curtissii* complex" by its minute capsules (1–1.5 mm long), which are shorter than or subequal to the sepal, its nectary disc of four flat greenish spots, and its reddish seeds. For detailed comparison, see Table 6.

Ludwigia microcarpa is uniform in reproductive structures but variable in vegetative habit. The stems are, as a rule, erect and usually well branched but are sometimes single. The stems and branches are straight or slightly zigzag. In outline, the plants may appear either narrowly oblong or narrowly rhombic when the plants are single or form short, subequal, ascending branches throughout the nodes; or they are triangular or ovate when the branches are gradually shorter from lower nodes up. The stems are normally annual and herbaceous; the plants may perennate either by forming stolons or by sending new shoots up directly from the spent stem base of the previous year. Woodiness is seen in some Florida specimens, presumably as a result of a favorable climate. The following specimen from Leon County, Florida, has an exceptionally woody base about 8 mm thick: sandy alluvium bordering wet woodland, Ochlockonee River, W of Tallahassee, *Godfrey 73131* (MO).

Most plants of *Ludwigia microcarpa* start to flower when young; it is common to find plants 5–10 cm high with flowers/fruits. The apetalous flowers are very small, with a tiny, greenish nectary disc from which a small amount of nectar is produced. Mechanical self-pollination apparently predominates in this species. In the experimental greenhouse, however, it has been successfully crossed to the diploid *L. linifolia* and *L. linearis*, tetraploid *L. glandulosa*, *L. lanceolata*, *L. polycarpa*, *L. sphaerocarpa*, and hexaploid *L. alata* and *L. simpsonii*; these combinations have resulted in the production of vigorous, floriferous hybrids (Peng, 1988). None set any seed. The F_1 hybrids between *L. microcarpa* and other petaliferous dip-

TABLE 6. Comparison of *Ludwigia microcarpa* with related species.

Characters	*L. microcarpa*	*L. simpsonii*	*L. curtissii*
Chromosome number	$n = 8$	$n = 24$	$n = 32$
Habit	Erect	Erect, ascending, or decumbent, occasionally prostrate and rooting at the nodes	Usually erect
Leaf			
Phyllotaxy	Alternate	Alternate except often opposite or subopposite in seedlings or at lower nodes	Alternate
Lateral veins (abaxial)	Slightly raised, conspicuous	Not raised, usually obscure	Not raised, usually obscure
Sepal length (mm)	0.9–2	1.2–1.8	1.5–3
Petals	Absent	Absent	1–3 vestigial petals occasionally present
Anther length (mm)	0.1–0.2	0.25–0.35	0.3–0.55
Filament length (mm)	0.4–0.55	0.55–0.8	0.75–1(–1.25)
Nectary disc			
Width (mm)	0.5–1.2	0.9–1.3	0.9–1.6
Elevated or flat	Nearly flat	Elevated as conspicuous bumps	Elevated as conspicuous bumps
Capsule			
Length (mm)	1–1.5	1.5–2(–2.5)	(2–)2.5–4(–4.7)
Width (mm)	1.4–1.9	1.5–3	2–3(–3.5)
Dehiscence	Ring-dehiscent	Loculicidal-dehiscent	Loculicidal-dehiscent
Bracteole			
Length (mm)	0.35–1.2(–1.5)	0.9–1.5(–2.5)	1.5–3.5(–4)
Width (mm)	0.1–0.4	0.35–0.85	0.4–0.8
Seed			
Color	Reddish brown	Light brown	Light brown
Surface cells	Transversely elongate	Transversely elongate	Tranversely elongate
Number/capsule	Ca. 10–20	Ca. 40–80	Ca. 50–150

loids were consistently petaliferous, suggesting that petal formation is controlled by a dominant gene. In other aspects, these F_1 hybrids were intermediate between their parents. Hybrids between *L. microcarpa* and species of higher ploidy level generally resembled the latter but tended to have smaller leaves and flowers.

Ludwigia microcarpa grows with *L. alata*, *L. curtissii*, *L. glandulosa*, *L. linearis*, *L. linifolia*, *L. pilosa*, *L. simpsonii*, and *L. sphaerocarpa*. Natural hybrids have been found between *L. microcarpa* ($n = 8$) and both *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$), both of which resemble *L. microcarpa* morphologically and share a common genome with that species (Peng, 1988). Since *L. simpsonii* and *L. curtissii* differ only in quantitative characteristics, which often overlap, it is impossible to distinguish between *L. microcarpa* × *L. curtissii* and *L. microcarpa* × *L. simpsonii* without knowing the chromosome number, or without seeing the populations in the field. These hybrids are usually readily recognizable by their erect stems; small and oblanceolate to spatulate leaves; apetalous flowers; elevated nectary discs; and minute, obpyramidal ovaries that abort after anthesis. The corners of the ovary/capsule often appear winged to some extent, apparently as a result of the aborted ovaries, which fail to develop into seeds in the locules of such hybrid individuals.

Hybrid populations between *Ludwigia microcarpa* and *L. simpsonii* are apparently common in Florida, where the two species grow in the same

habitats, often intermixed. These plants have a modal meiotic configuration of 8 bivalents and 16 univalents (Peng, 1988).

Confirmed hybrid populations of *Ludwigia microcarpa* × *L. curtissii* were found in Martin Co., Florida, 4.3 mi. E of Okeechobee and Martin county line, on FL 710, at Brady Ranch (*Peng 4202*, MO). Here they occurred along with putative parents by a wide depression between the highway and a railroad. Plants of *L. microcarpa* grew along the swamp border, whereas plants of *L. curtissii* stood in deeper water but were not as abundant as the former. Hybrid plants were scattered between them. The hybrids formed 8 bivalents and 24 univalents at meiosis (Peng, 1988).

Intersectional hybrid populations of *Ludwigia microcarpa* with *L. palustris* (sect. *Dantia*) were found in several counties of North Carolina, Georgia, and Florida (Peng, 1988). Their leaves were small, spatulate to broadly elliptic, alternate, subopposite or opposite; their flowers were small, apetalous, with minute ovaries, and aborting after anthesis; and the stems were prostrate and rooting at the nodes to ascending, suberect, or both. The combination of alternate leaves with a more or less prostrate habit in North American *Ludwigia* is usually indicative of hybridization between plants of sect. *Microcarpium* and sect. *Dantia*.

13. Ludwigia simpsonii Chapman, Fl. South. U.S., 2nd edition, suppl. 2: 685. 1892. TYPE: U.S.A. Florida: Manatee Co., Manatee, low ground, s.d., *C. T. Simpson s.n.* (holotype, US-1384069; isotypes, GH, MO in part, US—2 sheets). Figure 59.

Ludwigia cubensis Helwig, Repert. Sp. Nov. 25: 53. 1928. TYPE: Cuba. Piñar del Río: Remates, Ciénaga La Tumba, wet places, 16 June 1920, *E. L. Ekman 11304* (holotype, B, destroyed; isotypes, S—2 sheets).

Plants glabrous, erect, ascending, decumbent, or often prostrate and rooting at the nodes. Stems 10–60(–75) cm tall, well branched, leaf base slightly decurrent. Stolons rarely seen, new shoots arising from erect stem base or nodes of the trailing main stem, ascending at first, soon erect. Leaves alternate, those on lower nodes often opposite or subopposite, shape varied: spatulate, oblanceolate to very narrowly oblanceolate, or sublinear in extreme cases, 6–15(–20) mm long, (1–)3–7(–11) mm wide, apex acute or mucronate, margin subentire, with hydathodal glands, base attenuate into narrowly winged petioles 2–10 mm long. Stipules reddish purple, narrowly ovate-deltate, succulent, 0.15–0.25 mm long, 0.1–0.15 mm wide. Flowers in leaf axils, rarely congested. Sepals green with whitish, accrescent base, ovate-deltate, ascending, 1.2–1.8 mm long, 1–2 mm wide, apex narrowly acute or acuminate, margin entire. Petals 0. Anthers 0.25–0.35 mm long; filaments nearly translucent, 0.55–0.8 mm long. Pollen grains shed singly. Nectary disc green, raised 0.3–0.35 mm on ovary apex, 0.9–1.3 mm across, distinctly 4-lobed, glabrous. Style greenish, 0.25–0.4 mm long; stigma yellowish, subglobose, 0.15–0.25 mm thick. Capsules obconical, 1.5–2.5 mm long, 1.5–3 mm thick, comprising ca. 30–70(–100) seeds, glabrous or occasionally with minute, puberulent hairs ca. 0.05 mm long, sessile or with pedicels up to 0.4 mm long. Bracteoles attached on opposite sides near the base of capsules, lance-elliptic, 0.9–1.5(–2.5) mm long, 0.35–0.85 mm wide, swollen at base. Seeds light brown or brown, ellipsoid, 0.5–0.6 mm long, 0.3–0.35 mm thick, the surface cells transversely elongate, glabrous, occasionally covered by wax (?) taking the form of minute, appressed or ascending hairs. Self-compatible. Gametic chromosome number, $n = 24$.

Distribution. *Ludwigia simpsonii* occurs in sandy, peaty ditches, open pineland swamps, edges of cypress swamps, tidal flats or nearby marshes, and limestone sinks, sometimes growing as weeds, throughout most of eastern and southern Florida, with somewhat disjunct populations in the eastern part of the Florida panhandle and southernmost Mississippi (Fig. 60). This species also occurs in Cuba and Jamaica. Flowering and fruiting all year.

Representative specimens examined. U.S.A. FLORIDA: Bradford Co., New River, 1896, *Hitchcock s.n.* (F). Brevard Co., North Merritts Island, E side of Rt. 3, N of Wilsons Corner, *Shuey M1391* (USF). Broward Co., Fort Lauderdale, *Small & Carter 1171* (FLAS, GH, NY, US). Charlotte Co., Punta Gorda, *Curtiss 6757* (E, GA, GH, NY, S, US). Collier Co., Big Cypress, 6 mi. W of Miles City, *Brass 15832* (FLAS, GH, both mixed with *L. microcarpa*). Dade Co., 4 mi. SW of Florida City, *Thorne 14899* (USF, mixed with *L. microcarpa*). Duval Co., near Jacksonville, *Curtiss 930* (GA). Highlands Co., 1 mi. E of Highlands Hammock State Park, along Rt. 364, *Popenoe 1520* (FTG). Hillsborough Co., 4 mi. E of Dale Mabry on West Waters Ave., *Raven 18650* (DS, mixed with *L. microcarpa*). Lake Co., Eustis, *Nash 2136* (E, F, FLAS, GH, MO, MSC, NCU, ND, NY, US). Lee Co., Myers, *Hitchcock 117* (F, GH, NY, US). Manatee Co., Manatee, *Tracy 7602* (CM, F, GH, MO, MSC, NY, US, W). Monroe Co., Watson Hammock, Big Pine Key, *Killip 44454* (S, mixed with *L. microcarpa*; US). Palm Beach Co., near Jupiter, *Curtiss 5545* (C, E, FLAS, GA, GH, MO, MSC, NY, US). Pinellas Co., Fort DeSoto Co. Park, S of Gulfport, Hospital Key, Gulf of Mexico, *Lakela et al. 26366* (USF). St. Johns Co., St. Augustine, 1877, *Reynolds s.n.* (F, mixed with *L. lanceolata*; GH, mixed

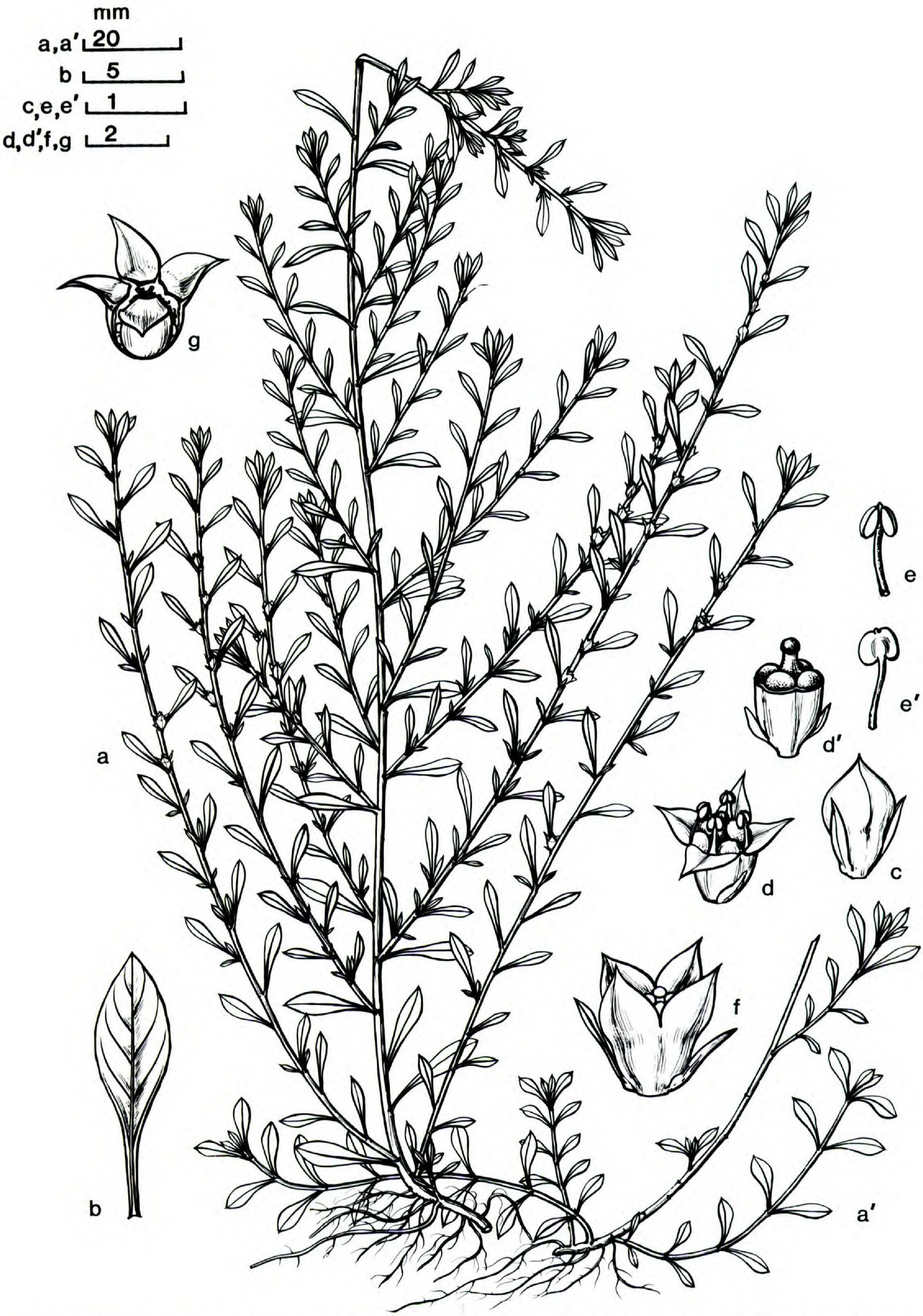

FIGURE 59. *Ludwigia simpsonii.* All but a′ from Florida (Collier Co., *Peng et al. 4272*, MO); a′ from Florida (Collier Co., *Peng et al. 4273*, MO).—a. Habit, erect stems.—a′. Basal ascending branches with some opposite

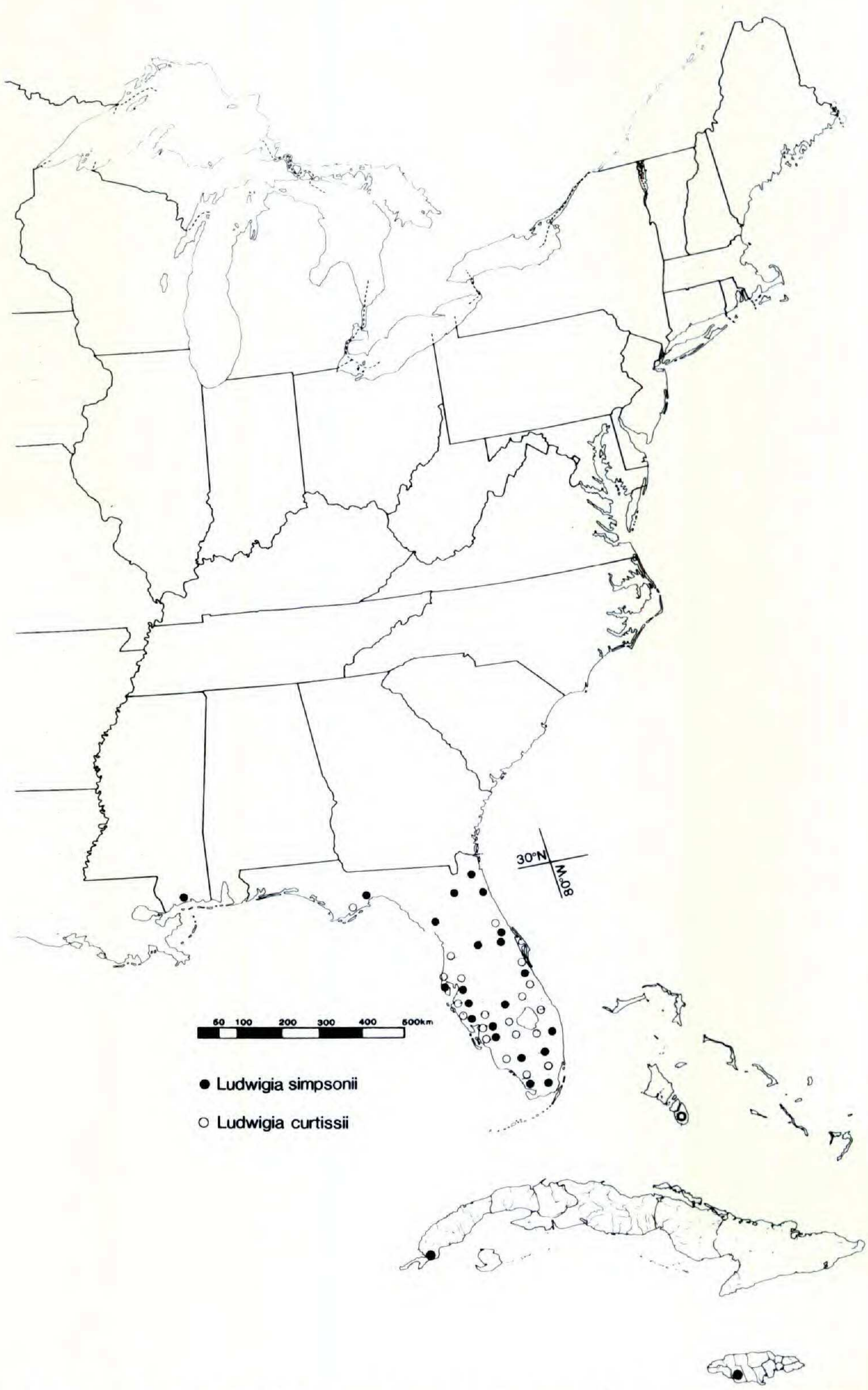

FIGURE 60. Distributions of *Ludwigia simpsonii* (closed circles) and *L. curtissii* (open circles).

with *L. microcarpa*; NY). Sarasota Co., 0.5 mi. E of W boundary of Myakka River State Park, on FL Hwy. 72, *Peng et al. 4313* (MO). Seminole Co., Sanford, *Nash 2278* (F, FLAS, GH, MO, NCU, ND, NY, US). Volusia Co., 6 mi. E of Geneva River on E side of St. John's River, *Kral 5171* (SMU). Wakulla Co., St. Marks, 1843, *Rugel s.n.* (NY, mixed with *L. microcarpa*). MISSISSIPPI: Harrison Co., Mississippi City, 1900, *Tracy s.n.* (MISS). CUBA. PIÑAR DEL RÍO: Remates, Ciénaga La Tumba, *Ekman 11304* (S). Cuba, *Wright 2554* (G). JAMAICA: near Black River, *Harris 9935* (BM, C, F, NY, P, RSA, US, Z). St. Elizabeth Parish, along the Broad River, 1 mi. below the Slipe Road Bridge, *Proctor 24836* (IJ).

Ludwigia simpsonii is very variable in habit and leaf shape. It, *L. curtissii* (including *L. spathulifolia*), and *L. microcarpa* form a closely knit

←

leaves.—b. Leaf.—c. Flower bud.—d. Flower.—d′. Partly dissected flower.—e, e′. Adaxial and abaxial views of stamen.—f. Capsule.—g. Dehiscent capsule.

polyploid complex, with the diploid *L. microcarpa* evidently having played a role in the formation of the other species (Peng, 1988). Its distinctiveness from the diploid *L. microcarpa* is readily perceived in capsule size, shape of nectary disc, seed color, and seed number per capsule. The characters separating *L. simpsonii* and *L. curtissii*, however, are nearly always quantitative and often overlap. Raven & Tai (1979) indicated that the diagnostic characters separating *L. curtissii* and *L. simpsonii*, such as capsule shape and size and leaf shape, are not correlated with chromosome numbers, and that the two species tend to converge in the experimental greenhouse. For reasons of this sort, these two species have frequently been merged under *L. curtissii* in the recent literature (e.g., Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982). By contrast, basing conclusions on abundant fieldwork and greenhouse and chromosome studies, I (1988) observed that the difference in chromosome number is correlated with mature capsule size. All plants with $n = 24$ have capsules 1.5–2(–2.5) mm long, whereas those with $n = 32$ have mature capsules (2–)2.5–4(–4.7) mm long. The morphology of plants with $n = 24$ fits closely the description of *L. simpsonii*, and the morphology of $n = 32$ plants clearly corresponds to that of *L. curtissii* (including *L. spathulifolia*). Comparison of these two species and the diploid *L. microcarpa* is in Table 6.

Although *Ludwigia simpsonii* and *L. curtissii* frequently are found in the same locality, they appear to be ecologically distinct and seldom occur side by side. *Ludwigia simpsonii* tends to grow along roadsides with other weeds in moist sandy soil. *Ludwigia curtissii* usually grows farther from roadsides, sometimes mixed with tall grasses or sedges, in black muck and often in deep standing water.

Ludwigia simpsonii sometimes grows with *L. alata*, *L. curtissii*, and *L. microcarpa*. Proven natural hybrids are known only of *L. simpsonii* × *L. microcarpa*; they occur in several scattered counties in Florida (Peng, 1988). These hybrids showed a modal meiotic configuration of 8 bivalents and 16 univalents and 4–24% stainable pollen. Their ovaries aborted after anthesis. *Ludwigia simpsonii* may form natural hybrids with *L. curtissii*, but such hybrids would be virtually impossible to pick out without studying their chromosomes and would probably be identified as one of their putative parents. Artificial hybrids between these two closely related species have been synthesized; they produced moderate numbers of seeds and had ca. 80–90% stainable pollen. They consistently showed a meiotic configuration of 24 bivalents and 8 univalents, which indicated that chromosomes of the three genomes in *L. simpsonii* pair with homologues in *L. curtissii*, leaving the eight additional chromosomes in this species unpaired. Based on morphological features and crossing relationships, the octoploid *L. curtissii* was probably derived following hybridization between a petaliferous, narrow-leaved diploid similar to *L. linearis* or *L. linifolia* and the hexaploid *L. simpsonii* (Peng, 1988).

Intersectional hybrids of *Ludwigia simpsonii* and *L. repens* ($n = 24$; sect. *Dantia*) have been found growing intermixed with both putative parents. These plants exhibited few, if any (0–1), associations of chromosomes at meiosis (Peng, 1988), which corroborated an earlier report by Schmidt (1967). The lack of chromosome pairing in hybrids strongly suggests that the three genomes of *L. simpsonii* are distinct from one another and are not homologous with any of the genomes present in *L. repens*. Judged by the fact that *L. simpsonii* often has opposite or subopposite leaves near the base of the stem or at the seedling stage, with a somewhat ascending, decumbent, or occasionally prostrate habit, it seems likely that it originated from hybridization between the diploid *L. microcarpa*, to which it is similar morphologically and with which it shares one genome, and a possibly extinct member of sect. *Dantia* with prostrate stems and opposite leaves.

Plants from the following collections are exceptionally fully prostrate and root at the nodes:

U.S.A. FLORIDA: Collier Co., 13 mi. N of U.S. 41, on U.S. 29, in vast grassy field behind roadside ditches (Big Cypress Swamp), *Peng 4268* (MO), *4273* (in part, MO).

They grow side by side with erect plants but are otherwise normal, small-fruited *L. simpsonii*, exhibiting 24 pairs of chromosomes in meiosis and setting abundant fruits with viable seeds.

Artificial hybrids between *Ludwigia simpsonii* and the diploids *L. linearis*, *L. linifolia*, *L. microcarpa*, the tetraploids *L. glandulosa*, *L. lanceolata*, the hexaploid *L. alata*, and the closely related octoploid *L. curtissii* have been synthesized, although with difficulty in some cases. Except for *L. simpsonii* × *L. curtissii*, which is highly fertile, all other combinations had 3–20% stainable pollen and produced very few, if any, seeds.

14. Ludwigia curtissii Chapman, Fl. South. U.S., 2nd edition, suppl. 621. 1883. TYPE: U.S.A. Florida: Brevard Co., ponds near Cape Malabar, July 1879, *A. H. Curtiss 922* (ho-

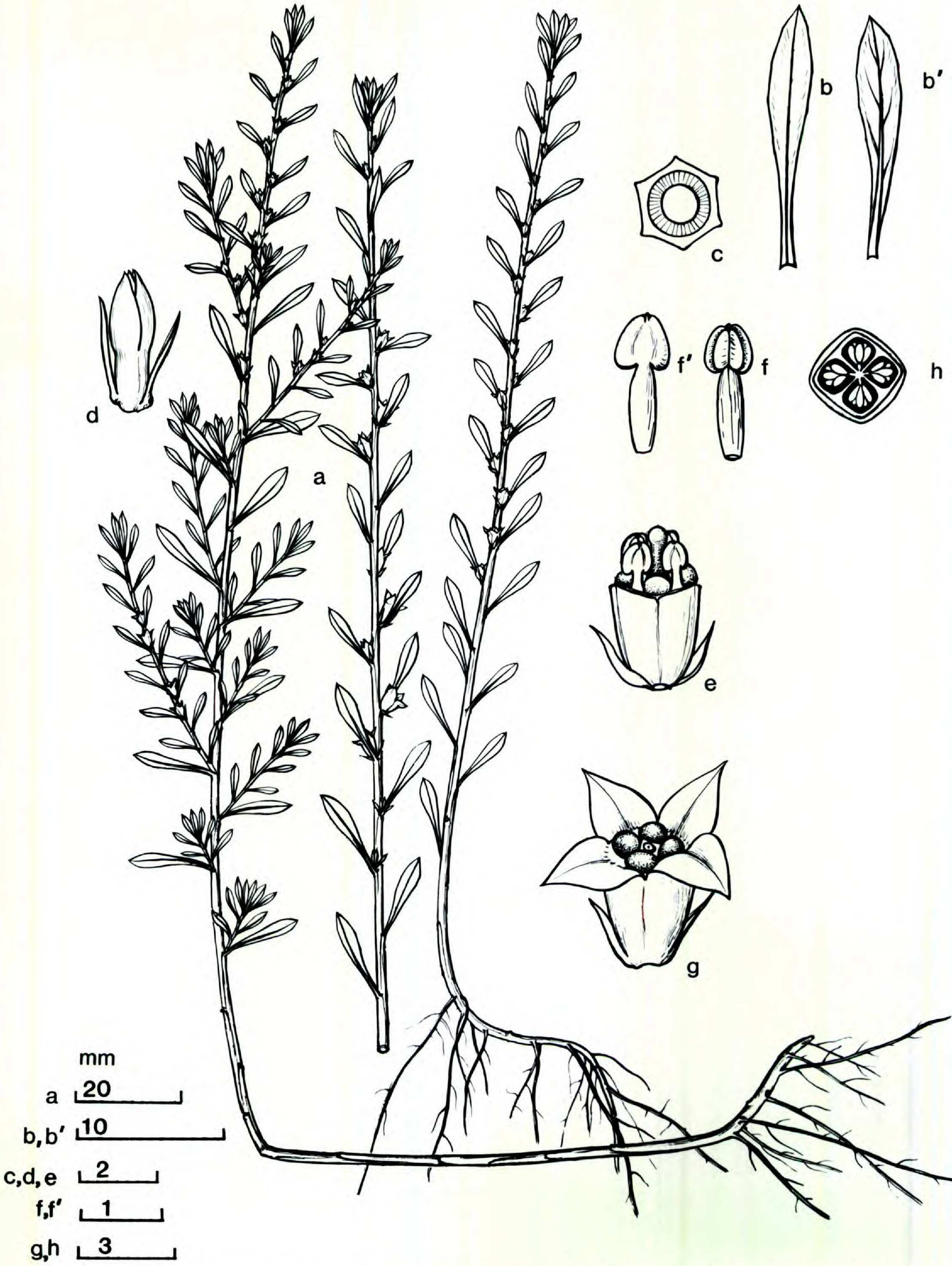

FIGURE 61. *Ludwigia curtissii* (Florida: Martin Co., *Peng et al. 4199*, MO).—a. Habit.—b. Adaxial and abaxial views of leaf.—c. Cross section of stem.—d. Flower bud.—e. Flower, partly dissected.—f, f′. Adaxial and abaxial views of stamen.—g. Capsule.—h. Cross section of capsule.

lotype, US-2630449; isotypes, BM, F, GH, M, MO—2 sheets, NY—3 sheets, PH, US). Figure 61.

Ludwigia spathulifolia Small, Man. Southeast. Fl. 943, 1506. 1933. TYPE: U.S.A. Florida: Dade Co., Everglades, northwest of Perrine, 16 Jan. 1909, *J. K. Small & J. J. Carter 2990* (holotype, NY).

Plants glabrous. Stems erect or ascending at base, very rarely creeping, 15–75 cm tall, single to well branched, the branches sometimes very slender; leaf bases slightly decurrent. Stolons not seen, new shoots ascending from base of the persistent, defoliated main stem of the previous year, very rarely prostrate and rooting at the nodes. Leaves variable in shape, most frequently oblanceolate-spatulate, sometimes spatulate or oblanceolate to very narrowly so, sublinear in extreme cases, 10–25(–30) mm long, 1.3–8 mm wide, glabrous, apex acute or mucronate, margin subentire with hydathodal glands, base attenuate into winged petioles 3–12 mm long. Stipules reddish purple, narrowly ovate, succulent, 0.2–0.3 mm long, 0.15–0.25 mm wide. Flowers in leaf axils, usually not congested. Sepals green with whitish, accrescent base, widely deltate or triangular, ascending, 1.5–3 mm long, 1.2–2 mm wide, apex narrowly acute or acuminate, margin entire. Petal usually lacking, 1–3 vestigial petals occasionally seen in some flowers, these yellow, narrowly elliptic, 1–2.5 mm long, 0.5–1 mm wide, apex obtuse, base attenuate. Anthers 0.3–0.55 mm long; filaments yellowish, 0.75–1(–1.25) mm long. Pollen grains shed singly. Nectary disc green, raised 0.3–0.4 mm on the ovary apex, 0.9–1.6 mm across, prominently 4-lobed, glabrous. Style greenish, 0.35–0.65 mm long; stigma yellowish, subglobose, 0.25–0.4 mm thick. Capsules obconical, (2–)2.5–4(–4.7) mm long, 2–3(–3.5) mm thick, glabrous, occasionally remotely minutely puberulent, the hairs 0.05–0.07 mm, pedicels 0.1–0.5 mm long. Bracteoles attached on opposite sides near base of capsule, narrowly lanceolate, lance-elliptic or oblong-linear, 1.5–3.5 (–4) mm long, 0.4–0.8 mm wide, swollen at base. Seeds light brown, ellipsoid, 0.45–0.6 mm long, 0.3–0.4 mm thick, the surface cells transversely elongate, glabrous, occasionally covered by waxes (?) that appear also like appressed or ascending hairs. Self-compatible. Gametic chromosome number, $n = 32$.

Distribution. *Ludwigia curtissii* grows in pine savannas and flatwoods, marshes, ponds, stream banks, sandy, peaty swales, limestone prairies, and in solution pits in limestone; it is restricted to the Bahamas and the peninsula of Florida (Fig. 60). Flowering and fruiting all year.

Representative specimens examined. U.S.A. FLORIDA: Brevard Co., near Eau Gallie, Indian River, *Curtiss 928* (FLAS). Charlotte Co., 3.5 mi. NW of Port Charlotte, *Godfrey 65356* (DS, DUKE, FLAS, FSU, LL, MSC, NCU, US, USF, VDB). Collier Co., Alligator Alley, picnic area ca. 5 mi. W of Miles City, *Avery 2039* (FLAS, mixed with *L. simpsonii*, FTG). Dade Co., Everglades, near Royal Palm Hammock, *Small et al. 6644* (FLAS, GH, NY, US). DeSoto Co., near Punta Gorda, *Bright 4541* (CM). Franklin Co., St. George Island, *Godfrey 71148* (FSU). Glades Co., 4.4 mi. SE of jct. of FL Hwy. 29 with US Hwy. 27, *Raven 18679* (DS, NCU). Hendry Co., 6 mi. S of La Belle, *Godfrey et al. 61009* (FSU, GH, SMU). Hernando Co., Choocochee Hammock, S of Brooksville, 1921, *Small et al. s.n.* (LL, NY). Hillsborough Co., old Memorial Highway, ca. 1.5 mi. from FL Rt. 580, NW of Tampa, *Lakela 25261* (FSU, GH, NCU, SMU, USF). Lee Co., 5 mi. N-NW of Ft. Myers, *Kral 7574* (FLAS, GH, US, USF). Manatee Co., Bradenton, *Tracy 7089* (MO, US). Martin Co., rd. between stable and exit, Jonathan Dickinson State Park, *Correll et al. 49914* (FTG, NCU). Monroe Co., 3.8 mi. W of Dade–Monroe county line, near FL Rt. 94, *Godfrey et al. 63519* (FSU, MO). Martin Co., W side of Big Pine Key, *Killip 41573* (F, NO, both mixed with *L. microcarpa*). Okeechobee Co., ca. 10 mi. N of Okeechobee, along US Hwy. 98, *Henderson 63-1621* (FSU, TEX). Palm Beach Co., NW of Loxahatchee in Corbitt Wildlife Management Area, *Kral 5636* (FSU, SMU). Pinellas Co., 4 mi. E of Clearwater, *Kral 7452* (FLAS, FSU, mixed with *L. palustris*, GA, GH, USF). Sarasota Co., 3 mi. S of Venice, *Kral 7495* (FLAS, FSU, GH, VDB). Volusia Co., 5 mi. W of New Smyrna, *Kral 18457* (VDB). BAHAMAS: South Andros, ca. 1 mi. SW of Congo Town airstrip, *Correll et al. 50247* (FTG, IJ, MO). Grand Bahama, Pelican Lake Area, *Correll & Popenoe 51315* (MO).

Ludwigia curtissii and *L. simpsonii* are both highly variable in habit and leaf shape and are often difficult to distinguish; the only consistent distinguishing character is the size of mature capsules. These two species are unique in sect. *Microcarpium* in having loculicidal capsules and in having, along with the diploid *L. microcarpa*, more or less spatulate cauline leaves. Their capsules dehisce by four longitudinally lenticular slits opposite the loculi. When dehiscence is complete, the capsule is split into four basally united parts topped with persistent but slightly shriveled sepals. This type of capsule dehiscence is highly specialized and has an anatomical basis (Peng & Tobe, 1987). *Ludwigia curtissii* and *L. simpsonii* are also distinct in that they are the only species in sect. *Microcarpium* that rarely produce true stolons. From the perennial base of the previous-year stem they form new shoots that ascend at first and soon become erect.

Some populations of *Ludwigia curtissii* from the Everglades of southern Florida and the Bahamas tend to have larger capsules (3.5–4.7 mm long) and were named *L. spathulifolia* by Small (1933). As their variation pattern closely parallels that of *L. curtissii* s. str., and they are octoploids with $n = 32$, they are here considered as variants of the slightly smaller-fruited *L. curtissii* that do not warrant taxonomic recognition, as was suggested by Long & Lakela (1976), Raven & Tai (1979), Godfrey & Wooten (1981), and Wunderlin (1982).

Ludwigia curtissii co-occurs with *L. alata*, *L. linifolia*, *L. microcarpa*, and *L. simpsonii* and hybridizes with the diploid *L. linifolia* and *L. microcarpa*, forming F_1s that form flowers but not seeds. *Ludwigia curtissii* × *L. microcarpa* exhibited 8 bivalents and 24 univalents at meiosis. The pollen stainability was 16% (Peng, 1988). As discussed above, natural hybrids between *L. curtissii* and *L. simpsonii* probably occur but would be difficult to recognize. Like *L. simpsonii*, *L. curtissii* forms intersectional hybrids with *L. repens* ($n = 24$, sect. *Dantia*) in the field. Such plants are vigorous and somewhat prostrate or suberect; they have alternate and opposite or subopposite leaves, but do not form viable seeds.

In the experimental greenhouse, artificial hybrids have been synthesized between *Ludwigia curtissii* and the diploid *L. linearis* and the tetraploids *L. glandulosa*, *L. lanceolata*, *L. pilosa*, *L. polycarpa*, *L. sphaerocarpa*, and *L. suffruticosa*. A few seeds were occasionally produced by some of the octoploid × tetraploid hybrids.

Compared with *Ludwigia simpsonii* ($n = 24$), *L. curtissii* ($n = 32$) is generally taller, more robust, more often erect, tends to have narrower and longer leaves, and nearly always has larger flowers and capsules. Further, the leaves of *L. curtissii* are nearly always alternate throughout, and the flowers occasionally have one to three vestigial petals. As these two species have three genomes in common (Peng, 1988), it is apparent that *L. curtissii* originated following hybridization between *L. simpsonii* and a diploid, petaliferous, erect species with narrow and alternate leaves, larger flowers, and longer capsules. The likely candidate for such a plant is only to be found in *L. linearis*, *L. linifolia*, the Cuban endemic *L. stricta*, or their progenitors. Indeed it is even possible that more than one of the above species hybridized with *L. simpsonii* in the past to form the present-day *L. curtissii*. If this is true, the morphological variability observed in *L. curtissii* is expected.

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